ASSESSING THE RELATIVE ROLE OF INTERNAL VERSUS EXTERNAL FORCING IN DRIVING PLANKTON COMMUNITY DYNAMICS IN EIGHT LAKE ONTARIO EMBAYMENTS

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ASSESSING THE RELATIVE ROLE OF INTERNAL VERSUS EXTERNAL FORCING IN DRIVING PLANKTON COMMUNITY DYNAMICS

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Population and community dynamics within ecosystems are driven by biological, chemical, and physical factors whose effects generally result from either external forcing: pressures originating from outside of the ecosystem boundaries (e.g., meteorological or anthropogenic in origin), or from internal self-organization: species interactions such as predation or competition. The aim of my research was to study the balance between these two general processes in plankton population dynamics and the relative impact of each in structuring aquatic pelagic communities.

I performed this research in eight embayments along the southeastern shoreline of Lake Ontario that varied widely in water residence time (WRT) because of differences in basin volume, watershed area, and degree of lake connectivity, where WRT was taken as in indication of the extent of external forcing. I used three approaches in this research: (1) seasonal characterization of plankton dynamics and community characteristics in each embayment along the WRT gradient represented by the embayments; (2) an intensive assessment of one external force, upwelling-driven exchange flow, on two embayments with similar connectivity, but different in volume and watershed size; and (3) mesocosm experiments that analyzed the factors responsible for the resistance of the plankton community in one embayment to the establishment of newly introduced species.

Overall, there was an underlying pattern of increasing internal self-

organization with decreasing WRT, although the relationship was complicated by the physical and biological characteristics of the embayments that buffered them from external forcing. For external forcing to be effective, it had to be sufficiently strong to counterbalance the dilution effect of large embayment volume or the flow-restricting action of dense macrophyte stands. Plankton community composition also counteracted the expected effects of WRT, as characteristics such as high plankton r_{max} allowed populations to respond quickly enough to high flow that they were able to thrive and interact, muting the expected wash-out dynamics. Additional trophic levels (fish, macrophytes) inhibited the potential disturbance of resident community dynamics by invading species. Overall, while external forcing played an important role in these systems, it was not as dominant a force as expected, highlighting the strength of internal self-organization in structuring plankton community dynamics.

BIOGRAPHICAL SKETCH

Rebecca Anne Doyle-Morin was born in 1977 on the shortest day of the year (the December 21 solstice), which likely explains why her days never feel long enough. She was fortunate to enjoy a farm-girl childhood, growing up with her parents John and Kathy and younger brother Joe on their farm in the rolling hills of the south-western Wisconsin driftless area. She spent her days outside, and had many of her first aquatic experiences exploring the frog-filled pond down the road with her brother, fishing for sunfish with her dad in the backyard creek, and boating around catching dinner with her grandpa on Shawano Lake.

Her love for all things ecological was nurtured in high school by her Biology teacher, Mr. Lorentz, whose lesson plans had her convinced that biology was all about ecology. Becky graduated as valedictorian of her Belmont High School class in 1996, and went on to do what she thought people interested in biology do: pursue a career in medicine. She started with her B.A. at Lawrence University. Here she was very fortunate to be assigned an ecologist as an advisor, Bart De Stasio, who convinced her to take his Aquatic Ecology class "for fun" in her third year of college. As it turned out, this course made Becky realize what was missing in her experiences with the medical field—the great outdoors! Becky switched her focus to the field of ecological research, and spent the next summer conducting research on Lake Winnebago's *Leptodora kindtii* population, which she turned into an honor's thesis entitled, *Assessing the Impact of the Invertebrate Predator, Leptodora kindti, on Daphnia pulicaria Population Dynamics in Lake Winnebago, WI.* This experience convinced her to pursue a career in ecological research, and so after graduating Magna cum laude from Lawrence in June 2000, she departed for Ithaca, NY, to pursue a graduate degree, which she is completing with this Cornell University thesis as part of Nelson Hairston's lab in the Department of Ecology and Evolutionary Biology.

Almost immediately upon arriving, she met a man by the name of Bryan Morin, who started as her bicycle salesperson and ended up her husband five years later. Also soon after arriving in town, Becky was offered the opportunity to join a large, multidisciplinary team as part of an NSF Biocomplexity grant that Nelson had just been awarded as part of a team of colleagues, and it was through this project that she developed and carried out her research on the embayments of Lake Ontario. A decade later, after many embayment adventures, and many personal adventures (including a marriage, a return to Wisconsin and to Lawrence, and a baby), the Big Red hockey team's biggest fan returned back to Cornell to defend and submit her thesis, wrapping up this chapter in her life.

In the meantime her life appears to have come full circle, as her return to Lawrence University as a Visiting Assistant Professor while writing has led her all the way home to southwest WI, where she will now continue to pursue a teaching and research career as a faculty member in the Biology Department at the University of WI-Platteville. She is also moving her family into her childhood home, and in addition to pursuing research at these sites, she is looking forward to collecting tadpoles and catching sunfish with her daughter, Elia, in the water bodies that initially inspired it all.

For my family…

be they the amazing crew I was born with,

or those I have acquired along the way,

I am so fortunate.

I love you all.

ACKNOWLEDGMENTS

Looking back on this experience and how I got to this point in my life, there seems to be an indefinite number of people who have truly affected me in a positive way, and who have played a part, both directly and indirectly, in the production of this thesis. There are so many, in fact, that it is certain that if I try to list them all, I will fail to mention countless very important people. And, so what follows is an attempt to thank those that I really could not have done this without, or, at the very least, who have routinely made it a particularly pleasant experience and have left me with many great memories of my time at Cornell.

I would first like to acknowledge the people and organizations that made my research logistically possible. The National Science Foundation provided the bulk of my research and stipend support through a graduate research assistantship that funded me as part of award OCE-0083625 from the "Biocomplexity in the Environment Program" to M. B. Bain, E.A. Cowen, S.P. Ellner, N.G. Hairston, and colleagues. Stipend support was also provided by funding from the Cornell Biogeochemistry and Biocomplexity Initiative, teaching assistantships from the Department of Ecology and Evolutionary Biology and Introductory Biology, and fellowships from the College of Agriculture and Life Sciences (including the Provost's Diversity Fellowship). Research support was provided by "small grant" funding to Kristi Arend and me from NSF IGERT "Biogeochemistry and Environmental Biocomplexity" to Cornell University, which covered many of the upwelling research expenses. I am very grateful to the PEO (Providing Educational Opportunities) organization, whose flexible award allowed me to get the computing equipment that I needed, as well as pay for some of the expenses incurred with my *Polyphemus* experiments. I am also grateful for the opportunity they gave me to speak at their state conference, which was a great experience. I am fairly confident that I will not speak in front of such a large

audience again for quite some time. I also received small grants from the International Association for Great Lakes Research and the American Society for Limnology and Oceanography, as well as Cornell's Graduate School, to help cover conference travel costs.

The other organizations that I would like to acknowledge are those that physically allowed us to do our research. Fairhaven State Park and the NY DEC were both incredibly accommodating, not only letting us use the boat launches and sample in their embayments, but also going out of their way to provide us with surface water temperature data and to help to guard my experimental mesocosms. There are a number of individuals who allowed us to use their private boat launches on a regular basis, which made our work much more convenient.

Of course, there are also the staff members that take care of the everyday logistics right in Corson Hall as well, and so I would like to thank the E&EB staff. My days unquestionably went more smoothly thanks to the department's administrative assistants and accountants, technical support, and maintenance crew. In particular, I would like to thank both Linda Harrington and Patty Jordan for their extra support during recruitment weekends, which I chaired for multiple years, and Dee Dee Albertson for all of her help with purchasing on my grant. I would also like to thank Brian Mlodzinski for his patience and help with my many computer issues, and Ron Wolverton for his assistance in keeping all of my electric equipment in working order. And, finally, I would like to give the custodial staff a special thank you for their cheery hello's and help with the doors in the wee hours of the morning when I was preparing to go into the field. They always helped to get my day off to a great start, and I certainly appreciated it!

I also received an immense amount of support from the faculty, students, and staff on Cornell's Lake Ontario Biocomplexity Project, without whom my research

could not have been completed. First, I would like to thank the principle investigators on the project for conceptualizing the project in the first place, and then working to get it funded. I would also like to thank them for all of their insight and support regarding my research throughout my time at Cornell. In particular, I would like to thank the Head PI Mark Bain for all that he did for me and for this project, but especially for keeping everyone motivated and moving forward. I collaborated quite closely with both Todd Cowen and Charley Driscoll, and expect to continue to do so as we work toward publishing this research, and I really appreciate all of the time and advice that I received from both of them, as well as the commitment to pursuing our collaborative projects (in particular the upwelling project) together. I appreciated the fact that Rolf Pendall included me in the brainstorming process for his survey project—opportunities to collaborate with faculty and students in the social sciences were one of the reasons I was excited to join this group for my thesis research. Both Bob and Steve were also invaluable P.I. resources for me, as I will describe below.

The project support staff were really the people that kept this project running and I owe a large debt of gratitude to them all for their enthusiastic and very effective efforts. In particular, Marci Meixler, Andrea Parmenter, and Gail Steinhart did an amazing job of coordinating the research and the overall project itself, while making sure we all had everything that we needed in terms of financial, equipment, data, and logistical or staff support. Their sincere interest in the success of this project, and in particular, the support they offered the graduate students, was truly appreciated, as has been their support even after they left the project. I could not have completed the intense fieldwork required of this project without such strong field support crew members, and in particular I would like to thank Tom Bell and Ethan Sobo for not only the many hours they helped out in the field, but also for their support and friendship—they worked very hard with me in some pretty tough conditions, yet we

got a lot done while having a great time every day we were out there together, and I really appreciate that.

Last, but absolutely not least for the Biocomplexity project is the support I received from the other students and post-docs on the project. Evan, Francisco, Javi, Nicole, Nong, and Xiaoxia were among the many post-docs and grad students who made this project both more fruitful and enjoyable for me, and from whom I learned a great deal. However, I absolutely could not have completed this research without the collaboration and friendship I had with my fellow "Biocomplexigals" Allie King, Kristi Arend, and Virginia Pasour (and their respective "Biocomplexiguys", Bruce, Eric, and Geoff). My professional interactions with them embodied the spirit of collaborative research and not only did I learn a great deal from each of them, but my dissertation is much stronger because I was able to work with them. The friendship that we have developed ranks right at the top of the relationships that I was fortunate to form while at Cornell, and I am so grateful for their sincere friendship and constant support and enthusiasm.

Another very important group of people that played an essential role in the completion of this research was the Hairston Lab group. A large bulk of my gratitude goes to two people here that I definitely could not have completed this research without and whose support went above and beyond—Colleen Kearns and Bob Johnson. Rumor has it that the Hairston Lab would not run without Colleen, and that's one rumor that could not be more true. The same is certainly true of Bob and the Ponds, and I am discussing the two of these people together because they rival for being, hands-down, two of the most supportive people that I have been fortunate to come across. I appreciate them both for their never-ending help and advice, both in the field and in the lab, and particularly for the long days they have both spent with me in the field. But, even more-so, I appreciate them for their friendship and constant

support. I truly cannot thank either of them enough for all they have done.

While the Hairston lab has been filled with a dynamic mix of incredibly bright and enthusiastic people the entire time I have been there, all of whom I would like to share my gratitude with for positively impacting both my research and me personally, Aldo, Becky P., Bill, Brian, Cayelan, Gretchen, Jake, Joe, Justin, Lutz, Mikael, Mike, Nancy, Ryan, and Take join the top of the list of lab research support, post-docs, grads, and undergrads who I would like to especially thank. This group has helped me with everything from phytoplankton and zooplankton identification to quantitative analysis advice to lecture prepping and field support, but beyond the knowledge and physical help that I have gained from them, these people have been incredibly supportive personally and have truly made the lab a great place to be (which was so important, considering the amount of time I spent there).

I did not spend all of my time in the lab however, and interactions with students, post-docs, and faculty outside of the Hairston lab were also such an important part of my life at Cornell. One of the reasons I chose Cornell was because of the interactions I witnessed between labs and among faculty and students across the department. From my cohort to my officemates, I really enjoyed and intellectually benefitted from the mix of students I interacted with on a regular basis. I am truly grateful to every student that I came across in the department and cannot even begin to list them all, but there are a few that certainly stick out and will certainly continue to be cherished friends for a long time. I was so lucky to start out with such an amazing cohort, and consider each of them to be dear friends. I would particularly like to thank a few that truly supported me when I needed it most, and continue to do so a decade later, including Angela, Brian, Curt (and Melea!), Katie, and Lauren, and particularly Jessica and Robert, who never ceased to know just the right thing to say or to do to make my day brighter. My office was also comprised of quite a cast of characters, all

of whom were always fun (and often informative as well) to interact with every day. I would especially like to thank Bryon, Gretchen, and Jeanne, who really became important mentors for me in addition to cherished friends. Of course, the list does not stop at my lab, cohort, and office, and I am particularly grateful for my continued relationships with friends like Dena, Jen, Krystal, Marissa, Marita…and the list goes on. I am not even coming close to mentioning all of the people I feel so privileged to consider friends from this great department…thank you all!

I'm also like to express my gratitude towards my very essential friends from outside of the department, including the fellow students I met teaching Introductory Biology (particularly Darlene, Jessica, and Tavis), the Biogeochemistry and Environmental Biocomplexity group (including Dana, Jim, Kathy, and Sam, among many), the migration of fellow Lawrence c/c alums that followed me to Cornell (including Eric, Josh, and Val), and of course, the hockey crew that spent their winter weekends screaming with me (especially Sean, Pete, Mike and Andrea, Allison and Rob, Mere and Ryan, and Tom and Sarah), and who soon became "year-long" friends!

And, finally, I would like to acknowledge the amazing faculty that I had the opportunity to work with at Cornell (that have not already been mentioned). Alex, Bobbi, Brian, Carol, Christy, Harry, Jed, and Keith were all particularly influential faculty that I was glad to get to know outside of my research. By example, each of them taught me about the kind of teacher and faculty member that I want to be. Harry, particularly, is one person who I am convinced lives to make others happy, and I really appreciate the fact that he never hesitated to stop and take the time to sincerely find out how I was doing, and to offer his encouragement, advice, and support.

I also owe a debt of gratitude to my committee members, Dick Root, Lars Rudstam, and Steve Ellner. While one of my regrets at Cornell has been not taking greater advantage of the really amazing committee members that I had, I have still

gained a great deal of knowledge, as well as some important new perspectives, from each of them, and their input has greatly improved my thesis. I am so grateful for Dick's participation on my committee, even into his retirement, because I think he brought a unique, broadened perspective to my research and to my training as a scientist that is hard to find anywhere else. Lars was also an instrumental member of my committee, particularly because of his extensive knowledge and background in the research that I was doing on Lake Ontario plankton, and because of this, he too was able to offer fresh perspectives on our data that we may not have considered (being too close to them). And, finally, I am grateful that Steve joined my committee, not only because of the mathematical expertise and understanding of my particular dataset and study system (as well as of Biocomplexity group dynamics!) that he brought to the table, but also because I think he brought a fresh perspective on how I should prepare myself for my chosen career in teaching in a way that really supported my end goal. All three members were both incredibly supportive and patient, particularly in these last few months, and I am truly grateful for all that they have done and the positive impact they have had on me in my professional development.

Last for the Cornell acknowledgements, but certainly not least, I would like to give my sincere thanks to my advisor, Nelson Hairston, Jr. I had a really hard time deciding where to pursue my Ph.D., and was fortunate to have some really strong options, but in the end, above all else, I chose to go to the school where I felt I would have the strongest advisor—a person who could best support me as I grew as a scientist and scholar, particularly given my broad interests and relatively recent focal switch to pursuing an ecological career. Looking back, there is no doubt in my mind that I made the correct choice. I truly respect Nelson for the high quality and exciting research he does (and the great stories he tells with it), and for his impressive teaching ability, but above all, I have learned to really appreciate Nelson most for the sincere

person that he is. I am constantly amazed with how much he balances in his career, and yet how he somehow always finds a way to give everything his full effort and attention. He has truly supported me in every way through this experience, and because of him, I have been able to take so many opportunities that have truly shaped the person that I have become (and am still becoming!). It is clear that he has always had my best interests in mind, and I truly appreciate everything he has done for me.

My gratitude is certainly not limited to the Cornell campus, and I would like to briefly acknowledge the many others who deserve credit for helping me get to this point in my career. I would not have even considered Cornell for graduate school, and I am not convinced that I would have gotten my new position at University of Wisconsin, Platteville, if it had not been for the advice and the support of Bart De Stasio. In fact, I probably would not be pursuing a teaching career in Ecology at all if it had not been for him. I am grateful for his inspirational teaching, and the very insightful advice he gave me as an undergraduate student at Lawrence, as well as all of the opportunities he gave me to prepare for a research career once I had decided on that path. I appreciate that he "kept tabs" on me through the years, and that once he realized I was considering a teaching career, that he considered me to fill his position as a sabbatical replacement at Lawrence, which was just the experience I needed to feel confident about pursuing a teaching career. Bart truly represents the "Lawrence difference", and I am grateful to have such a great mentor and role model in my life.

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And finally, I chose to dedicate this to my family, because I truly would not be writing this now if it was not for their amazing support. Many friends (including some mentioned above) would certainly fall into the category of "acquired family". Two that certainly fit that bill would be my dear childhood friends, Beck and Tam (and their families). These two have heard it all and offered wonderful advice and much needed hugs along the way—truly more like sisters than friends, they are both great examples of what a true friend is, and I am so lucky to have them in my life. Bryan's close childhood friend Greg, also falls in this category, and I have really appreciated the great philosophical conversations we have had about the science of biology and about life in general.

I am also incredibly fortunate to be so close to my extended family, which has doubled in size since starting my dissertation with the addition of my in-laws; it is not surprising when you meet our families that Bryan and I have not been on a solo vacation for nine years because we have chosen to spend all of our vacation time with them. They are a truly wonderful group of people that have fully supported me through every step of this process, and have been a constant reminder of what is truly important in life along the way. I would particularly like to thank my 96-year-old grandmother, who never fails to remind me of how proud she is of me (even though she admits that she is not quite sure what I am doing); she may be impressed with the degrees I am pursuing and the career I am building, but I think that the life that she has

led and the person that she has become are much more admirable, and certainly something that I strive towards.

Finally, I would like to thank my immediate family. I am so thankful to Bryan's family for immediately and fully accepting me into their circle and for their continued support. Bryan and I have amazing siblings. While I apparently asked my parents to exchange him for a sister, I am glad they decided to bring my brother Joe home from the hospital anyway. We may not talk on the phone every day or know exactly what is going on in each other's lives at all times, but we have a really great friendship that I truly cherish. Without realizing it, Joe really pushes me to be a better person and to strive for more in my career and in my life and I really appreciate the fact that he is always there when I need him. I was lucky to get another brother and the sisters I always wanted when I married Bryan, and I have really enjoyed getting to know them all. I am especially grateful for the time that we had with Bryan's sister Michelle and her family while living in Ithaca. It has been really great for us to share in the experience of watching her children grow up, and I thank the budding scientists, Ana Maria, Miguel, and Tomas for constantly reminding me of how fun and amazing science is. As the only family that truly understands what I was undertaking, having been there themselves, Michelle and Juan provided an important source of support and understanding throughout the process.

Finally, the people that I can give the most credit to, in terms of getting me to this point today, are my parents, husband, and daughter. My parents have instilled me with a strong balance of appreciation for where I have come from and a sense of independence and an inner drive about where I am going. While they were quite clear about the fact that they were not happy about my decision to move to Ithaca to pursue this degree (and turn down my second choice—nearby Madison), it certainly did not stop them from being two of the most supportive parents I have met. I particularly

appreciated their annual trips out to visit, and I know that none of us will forget the day—9/11/01—that they spent in the field with me. I know that they did not understand why I chose to pursue my degree at Cornell, or why I was in Ithaca for so long, and until I became a mother, I know that I did not understand their perspective on my choices either, but I do know that we are all thrilled that the path I took has allowed me the chance to head back home. Above all, I am so glad that my daughter will also have the opportunity to grow up with these amazing people routinely in her life.

And, of course, there is Bryan. He is the one person who has physically and emotionally been by my side through almost all of this—essentially, he just missed out on the initial move to Ithaca, since we met my first day in town. While I am not sure that I believe in fate, this would be the one case that would convince me. He is certainly not the person I would have initially seen myself spending the rest of my life with, but as it turns out, he is exactly the kind of person I need to be with. I am truly grateful to his mother, because I see so much of her kind, giving spirit in him, making him a truly great partner. I particularly appreciate Bry for finally being the impetus that I needed to strike a balance between my work and personal life, and to view my career as only a small (but important) part of the larger picture. Regardless of what steps I have taken and decisions I have made, he has been a constant source of support and comfort. I am most grateful to him for convincing me to start considering children. While the timing was not exactly what we had planned, I could not be more happy to have had Elia literally by my side throughout this past year. She has been such a source of inspiration to me and has completed the task her father started of motivating me to take the time to consider my life in a broader perspective and to begin to prioritize what really matters. I am truly fortunate--thank you, all.

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CHAPTER 1

INVESTIGATING THE ROLE OF WATER RESIDENCE TIME AS A DRIVER OF PLANKTON COMMUNITY COMPOSITION AND DYNAMICS

Introduction

Species dynamics within ecosystems are driven by a variety of biological, chemical, and physical factors. Populations change in response to biological interactions such as predation, competition, parasitism and symbioses (Hairston et al. 1960, Connell 1961, Janzen 1966, Paine 1971, Addicott 1974, Rothstein 1975, Hairston 1980, Morin 1983, Clay et al. 1985, Root and Cappuccino 1992, Cáceres et al. 2006), by altered nutrient cycling through the system (Likens 1971, Wimp et al. 2010), and through major physical disturbances (Sousa 1979, Hughes 1984, Sousa 1984). In lakes, plankton population dynamics are externally forced (driven from outside the shoreline boundaries) by temperature, wind, and precipitation events (De Stasio et al. 1996, Winder and Schindler 2004, Gyllström et al. 2005, Doyle-Morin et al. Chapter Two), influxes of nutrients from the landscape (Edmondson 1970), and introductions of exotic species (Lehman 1991, Schulz and Yurista 1999, Benoît et al. 2002). From within the aquatic system, internal dynamics result from nutrient recycling (McCauley and Kalff 1987, van Donk et al. 1993), interspecific competition (MacIssac and Gilbert 1991, Goulden et al. 1982), grazing pressure (Porter 1973, Lampert et al. 1986, Sommer et al. 2003), predation (Brooks and Dodson 1965, Lynch 1979, Schindler 1987), and changes in habitat structure (Gliwicz 2003). While some combination of these influences work simultaneously in each pelagic ecosystem, the significance of each, their seasonal timing, and particularly the relative importance of

internal dynamics versus external forcing for dynamics varies as a function of the extent to which a plankton community is connected to the external environment.

Embayment ecosystems – bodies of water that have a direct connection to a larger, adjacent body of water – provide the ideal opportunity to study this balance between internal self-organization and external forcing. Along the shoreline of very large lakes, such as the Laurentian Great Lakes, embayments are abundant and often within close geographic proximity to one another. Such water bodies provide an opportunity to study systems with different levels of connectivity, but that experience similar climatic impacts and have access to the same regional planktonic taxa. In addition, the variation in the strength of connection to the large lake that defines these systems as embayments, as well as differences in embayment volume and in connectivity to the surrounding terrestrial landscape, make it possible to explore a wide gradient of impacts from external forcing.

We explored the patterns of plankton community composition and dynamics in eight embayment systems located on the southern and eastern shorelines of Lake Ontario (Fig. 1.1) that vary in total volume (between 8.90×10^4 m^3 and 2.92×10^7 m^3), connectivity to Lake Ontario (ranging from a permanently maintained channel to only indirect seepage through a gravel bar), and watershed area (1.0 to 3658 km^2) (Table 1.1a). This combination of characteristics created a gradient in external forcing through their combined effect on water retention time (WRT) – the mean amount of time water, dissolved chemicals, and suspended substances entering an embayment stay in that water body before exiting by flow into the larger lake. Using this WRT gradient (between 1 and 148 days for our eight embayments), we explored how the magnitude of external forcing influences plankton dynamics.

Previous research conducted in laboratory flow-through microcosms (chemostats) has shown that WRT is an important driver of zooplankton-

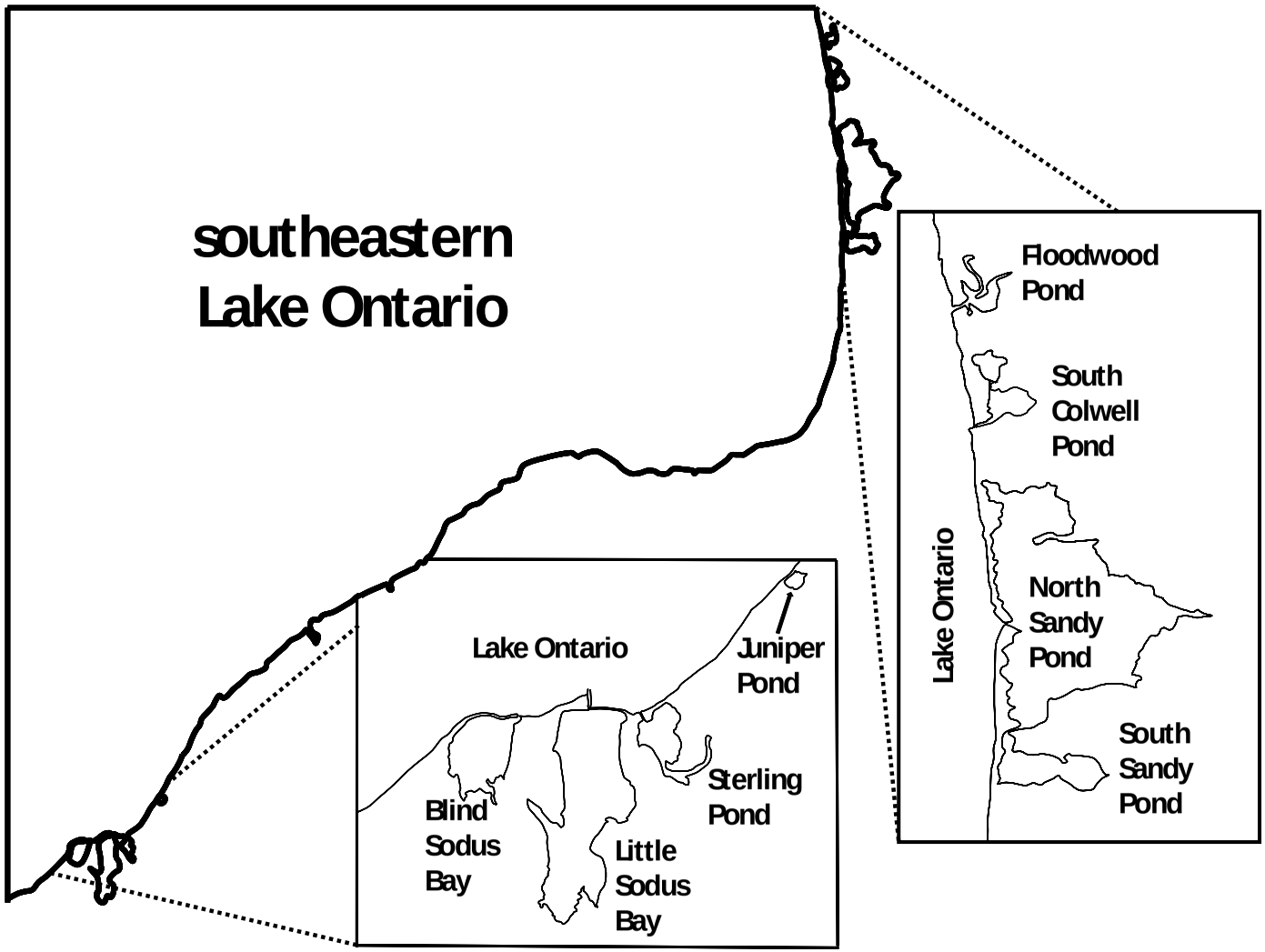


Figure 1.1 Map of eight L. Ontario embayments

Table 1.1 Physical (a), chemical (b), and biological (c) characteristics of L. Ontario embayments (Cornell University 2010, C.T. Driscoll personal communication, Arend 2008).

a) Physical	**Maximum Depth (m)**	**Volume (m^3)**	**Watershed Area (km^2)**	**Watershed % Agriculture**
Blind Sodus B.	7	4110326	36	37
Little Sodus B.	11	20242177	12	17
Sterling P.	3	991331	203	43
Juniper P.	3	88985	1	40
South Sandy P.	6	4303587	10	29
North Sandy P.	5	29185426	246	24
South Colwell P.	3	844857	2	19
Floodwood P.	5	247493	3658	37

Table 1.1 continued

b) Chemical	N load (kg year^{-1})	P load (kg year^{-1})	Watercolumn Total N (μmol L^{-1})	Watercolumn Total P (μmol L-1)
Blind Sodus B.	17901	523	38	1.34
Little Sodus B.	3127	29	23	1.01
Sterling P.	113876	3595	52	1.66
Juniper P.	352	11	39	0.64
South Sandy P.	6692	163	38	0.67
North Sandy P.	147970	2879	28	0.64
South Colwell P.	875	10	43	0.86
Floodwood P.	549994	15942	53	0.69

Table 1.1 continued

c) Biological	**Planktivore Biomass (g min^{-1})**	**Piscivore Biomass (g min^{-1})**
Blind Sodus B.	890	17029
Little Sodus B.	2588	13365
Sterling P.	5519	15640
Juniper P.	74	79
South Sandy P.	7154	12516
North Sandy P.	735	7514
South Colwell P.	1509	10057
Floodwood P.	5566	8597

phytoplankton dynamics (Fussmann et al. 2000; 2005). Varying dilution rate, the speed at which growth medium is pumped through these artificial systems (i.e., in effect WRT), in combination with external enrichment (limiting nutrient concentration) determines whether predator-prey microcosm food chains exhibit predator-prey cycles, stable coexistence, or extinction. The patterns observed in these simple communities illustrate how the balance between external forcing (WRT) and internal self-organization (the strength of interspecific interactions) dictates the resulting plankton dynamics. Our embayments, with their varied "flow-through" rates due to their differing connectivities to their watersheds and Lake Ontario, offer an opportunity to explore these questions at a much larger and more natural scale.

Plankton dynamics in embayments with low vs. high water retention time

Although we do not really believe that embayments are large chemostats, these field systems do have some properties in common with continuous flow laboratory microcosms: inflow of nutrient-rich medium (typically primarily via one or a very few single inlet streams); a relatively constant volume in which plankton taxa at several trophic levels interact; a single outflow that exports both embayment water and the plankton it contains. There are, however, many ways in which they are more complicated than chemostats: for example, benthic-pelagic coupling of nutrients and organisms at the sediment-water interface; shallow areas and complicated shorelines with the potential for significant growth of submersed and emergent macrophytes; higher trophic levels such as fish that have generation times much longer than that of the plankton and that are able to avoid being flushed out; non-constant external forcing from variable rainfall, wind, and human activities in the watershed.

If the analogy with chemostat dynamics holds at all, we would expect the interactions among pelagic resources and consumers to differ between high and low

WRT embayments. Very generally, this means that all else being equal (i.e., the same assemblage of taxa in all embayments and unimportant seasonality), where WRT is high there should be tight internal coupling among species with reciprocal interactions between consumer and consumed, and negative interactions among species within a trophic level. In contrast, planktonic taxa in externally driven, low WRT systems should be positively correlated in abundance, with consumer and resource species fluctuating together, driven to low densities by high flushing events and recovering together once an event ends. Nutrient influxes from the watershed during events may stimulate growth, but strong biotic interactions would have little or no time to develop before the next flushing event. The larger the variation in external forcing, the more tightly we would expect plankton dynamics to be positively correlated in low WRT embayments.

This simple embayment-as-chemostat hypothesis was motivated in part by preliminary data collected during a heavy precipitation event at the end of 2001. After a dry summer, a week-long rainstorm in late September flooded the watersheds of all of our study embayments. An exploration of phytoplankton and zooplankton dynamics in two embayments representing opposite extremes of WRT illustrates the patterns just discussed. Floodwood Pond, which is highly connected to its watershed by a series of tributaries draining a large watershed (3658 km^2), and has a strongly flowing natural channel connecting it to Lake Ontario, represents a system with a low WRT. Its phytoplankton and zooplankton communities were both completely washed out as a result of the flooding event (Fig. 1.2a). In contrast, Juniper Pond, with very low connectivity to the surrounding landscape (1 km^2 watershed area) and no channel connecting it to Lake Ontario (the only flow to Lake Ontario is via percolation through a gravel bar), showed phytoplankton and zooplankton community dynamics that appear to fluctuate oppositely to each other (Fig. 1.2b), suggesting that the plankton

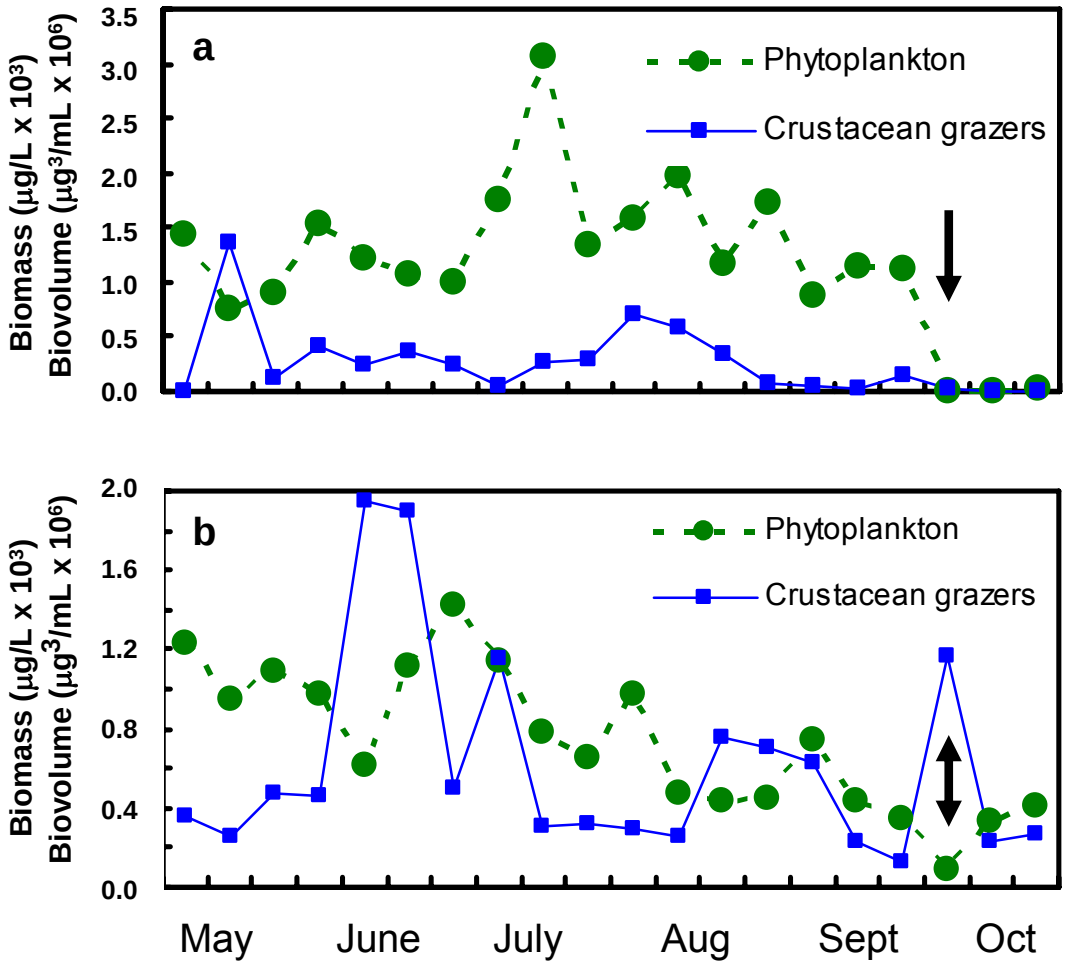


Figure 1.2 2001 phytoplankton and crustacean grazer dynamics in low WRT embayment Floodwood P. (a) and high WRT embayment Juniper P. (b). The flooding event occurred on 25 September, as indicated by arrows.

dynamics were driven mostly by internal biological forcing. At least at the extreme ends of the WRT gradient and under high runoff, the chemostat analogy seems useful. Our question here is: How far does the analogy go?

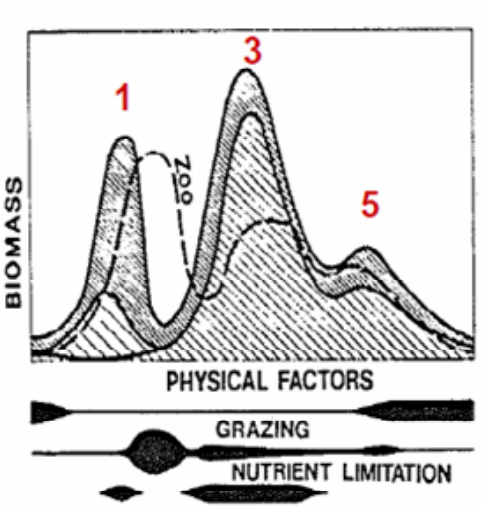
The plankton of embayments may differ from chemostat communities in several critical ways. First, natural water bodies are subject to strong seasonal changes in solar insolation and the effects that this has on primary production as well as on water temperature, thermal stratification, and related physical and chemical (nutrient) processes (Wetzel 2001). Second, the taxonomic composition of the plankton, and especially the dominant functional groups, may differ among embayments in ways that influence the nature of how sensitive plankton dynamics of any particular system are to the temporal mean and variance of WRT.

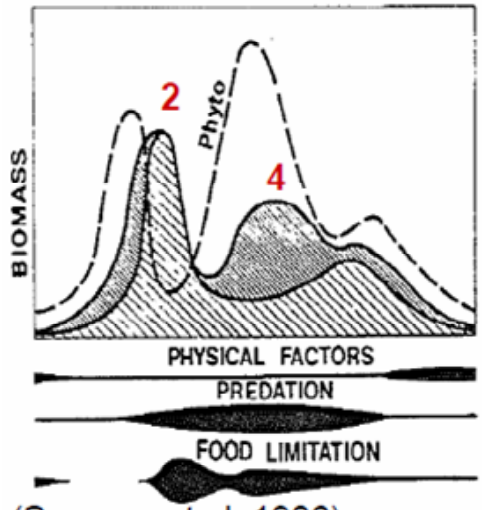
In high WRT systems, changes in phytoplankton and zooplankton populations should be underlain by consumer-resource dynamics, modified by seasonal forcing driving species succession. A general depiction of the seasonal plankton dynamics of North Temperate Zone lakes of intermediate size and moderate to high productivity is that described by the Plankton Ecology Group (the so-called PEG Model: Sommer et al. 1986). The most pervasive example of consumer-resource coupling in these lakes is the clear water phase (CWP) in which the annual spring phytoplankton bloom is terminated by an increase in the abundance of grazing zooplankton, especially members of the genus *Daphnia* (Lampert et al. 1986, Sarnelle 1993, Scheffer et al. 1997). The CWP typically starts in late May or early June, though the timing may vary, and ends when *Daphnia* abundance declines as a result of some combination of limiting abundance of phytoplankton (Threlkeld 1979), a seasonal shift in phytoplankton composition toward poor quality taxa such as cyanobacteria (Arnold 1971, Trabeau et al. 2004), and a seasonal increase in the density or activity of zooplanktivorous fish (including young of the year) (Luecke et al. 1990, Rudstam et

al. 1993, Klumb et al. 2003, Wagner et al. 2003, Hansson et al. 2007a). Other common traits of seasonal phytoplankton and zooplankton succession that are representative of internally-driven dynamics (outlined in Fig. 1.3) include the mid-summer appearance of cyanobacteria as the water column becomes N-limited, as well as large silica-dependent species blooms during fall overturn as the temperature cools and photic zone receives silica from mixing with the hypolimnion (Sommer et al. 1986). The mid-summer *Daphnia* decline is often followed by an increase in the abundance of selective zooplankton species, including copepods and small cladocerans, which are released from competition with *Daphnia* and better adapted for selectively obtaining good food particles from a phytoplankton mixture that contains many poor food species (Kirk and Gilbert 1992, Hansson et al. 2007b). We expect the CWP and these other competition-based lake succession patterns to be more prevalent in high WRT than low WRT embayments.

Fundamental to any expectation about how WRT influences plankton dynamics however, must also be a consideration of the characteristics of the species present, especially their potential maximum growth rates. If species composition remains essentially constant, the effect of decreasing WRT should be an increase in the importance of external forcing (as is the case in simple laboratory chemostat communities; Fussmann et al. 2000, 2005). Similar plankton communities in these different systems are not entirely unlikely, given the close geographic location of the embayments to each other and their connection to the same large lake. However, plankton assemblages may also be a product of local differences in the physical, chemical, and biological environments of individual embayments. In particular, the plankton dynamics in an embayment should be as much a product of the growth rate characteristics of the species present as they are of WRT (or any other environmental variable). If species with short generation times and high growth rates are what persist

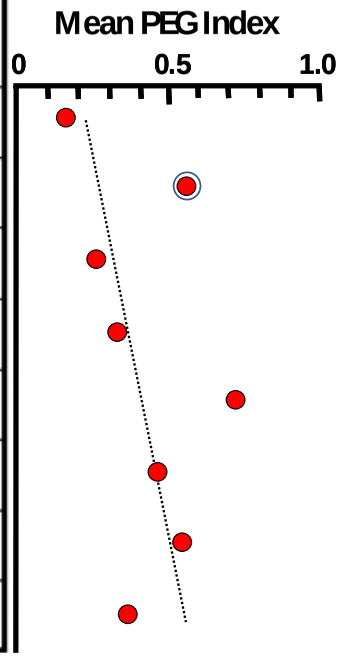
Figure 1.3 Common characteristics of plankton succession in (eutrophic) lakes expected in high WRT systems (adapted from Sommer et al. 1986). The Sterling P. outlier is circled. ρ (2.218*) is significant at the $p \leq 0.10$ level when outlier removed.





(Sommer et al. 1986)

		1	2	3	4	5
Expected (High WRT)		Spring edible phyto-plankton bloom	Early summer *Daphnia* species increase	Late summer N-fixing cyano-bacteria bloom	Late summer copepod increase	Fall turnover edible phyto-plankton bloom
FL	Low WRT	0	0	0	0.7	0
ST		0.9	0	1	0.8	0
NS		0.7	0.4	0.1	0	0.1
LS		0.5	0	0	0.6	0.4
BS		0.9	1	0.1	0.4	1
SC		1	0	0.4	0.7	0
SS		0.8	0.5	1	0.1	0.1
JU	High WRT	0.6	0	0	1	0



in embayments with low WRTs while those with long generation time and relatively slow growth rates dominate in high WRT embayments, any differences in plankton dynamics among embayments may be reduced or eliminated.

If a species' characteristics are important in explaining in which embayments it occurs, we expect to see a phytoplankton community dominated by small, fast-growing, edible species in low WRT habitats. These organisms, which include species predominantly in the Chlorophyta, Chrysophyta, Bacillariophyta and Cryptophyta, grow quickly in response to high nutrient conditions and are easily handled and digested by grazing zooplankton. Silica-dependent diatoms and some chrysophytes are also common in the physically turbulent conditions that often accompany nutrient introduction, typical of spring and fall turnover, both because dissolved silicate enters the water column, and because turbulence aids in keeping the cells, heavy with silica-laden frustules, suspended in the euphotic zone. External physical forcing in the low WRT water bodies, especially from the intrusion of cool water during summer, could have a marked effect on diatom and chrysophyte populations, generating a bloom outside of the spring or autumn bloom periods as long days and added nutrients stimulate growth of taxa that typically do best at low water temperatures. These species could present an exception to the small size expectation just described, given that many grow as large cells or colonies (e.g., *Dinobryon*, *Fragilaria*).

The small-bodied, high r_{max}, zooplankton taxa that we expect to see in low WRT systems include rotifers and small cladocerans (e.g., *Bosmina, Chydorus*), all of which are parthenogenetic for much of the growing season. Because larger, slower growing taxa such as *Daphnia* and copepods (Koivisto and Ketola, 1995) are likely to be unable to persist in these high dilution-rate environments, their importance as dominant competitors (Lynch 1979, Goulden et al. 1982, Vanni 1986), or effective predators (e.g., cyclopoid copepodids (Dodson 1974), calanoids and *Daphnia* that

consume rotifers (Williamson 1986, Gilbert 1988a,b, Conde-Porcuna 1994)) is diminished, allowing the smaller taxa to thrive. Nevertheless, although embayment waters are often nutrient-rich due to the continual influx of water from surrounding farm land, and shoreline septic fields, even small taxa may not reach high population sizes very quickly, or ever in these seasonal environments, if their realized growth rates are low because of high wash-out rates in low WRT conditions.

In high WRT systems, where we expect physically forced population loss rates to be relatively low, ecological interactions like competition and predation will likely be significant drivers of plankton dynamics. There are, however, a number of organisms that we would expect to see established only in systems with these low washout rates due to their particular adaptations. These include the largest and least edible phytoplankton taxa such as cyanobacteria, which often dominate in calm high WRT conditions (Paerl and Huisman 2009, Soares et al. 2009, Elliot 2010), especially where phosphorus is enriched favoring N-fixing species**.** Together with cyanobacteria, the phytoplankton expected in higher WRT systems, include dinoflagellates, colonial greens, and chrysophytes, which are defended against grazing by some combination of large cell size, gelatinous sheaths, spines, thick cell walls and toxins. These defenses require energy investment that correlates with reduced r_{max} (Agrawal 1998), again making these taxa less able to persist in high-flushing low-WRT embayments, but well suited to high WRT systems where biotic interactions are more likely to be intense.

Zooplankton that do well under conditions of intense competition or predation tend to be slower growing and longer-lived. One genus that we expect to be well represented in high WRT systems is *Daphnia*. Their large size and generalist feeding behavior allows them to filter water efficiently, limiting resources for the smaller cladocerans and rotifers (Vanni 1986). However, generalist feeding is only beneficial

when phytoplankton is dominated by high food-quality taxa, typical in most freshwater pelagic systems early in the growing season (Sommer et al. 1986). In the presence of the poor food-quality taxa expected to dominate high WRT embayments, copepods, another slow-growing long-lived group, should become dominant because of their ability to feed selectively, avoiding phytoplankton of poor food quality (Kirk and Gilbert 1992, Hansson et al. 2007b).

This recounting of possible mechanisms regulating plankton dynamics along a gradient of WRTs, suggests two alternative patterns at the extremes: (1) if community composition remains relatively constant among embayments, we expect to see the effect of external forcing dominating in low WRT conditions and then diminished at progressively higher WRT embayments as the importance of interspecific interactions increases, whereas (2) if instead species composition varies among embayment ecosystems, as is likely, so that high r_{max} taxa dominate in low WRT systems and low r_{max} taxa in high WRT systems, then the ratio of species growth rate to average wash-out rate may not vary nearly as much as the first alternative would suggest, and the plankton dynamics (assessed as changes in aggregate groups such as all edible phytoplankton and all grazing zooplankton) might not be very sensitive to a gradient of WRTs. We expect that these patterns cannot be considered strictly as alternative hypotheses, because they are not mutually exclusive and intermediate mixtures of the processes are possible.

Methods

This research is a component of a larger study of the dynamics of embayment ecosystems along the Lake Ontario coast, including, in addition to the plankton addressed here, hydrodynamics, nutrients and other water chemistry, macrophytes and fishes. The primary monitoring dataset for this study was collected though weekly

sampling between 8 May and 8 October, 2002, while focused process studies were carried out in other years (Chapters 2 and 3). Methods for plankton collection and analysis are detailed below, while nutrient, macrophyte, and fish data collected at the same sites and on the same dates as the plankton will be described in detail elsewhere (C.T. Driscoll personal communication; R.L. Johnson personal communication; Arend 2008), but are mentioned here to provide context.

Site Descriptions

The eight embayments of this study are located in two groups of four, one on the southeastern shoreline, and the other on the eastern shoreline of Lake Ontario (Fig. 1.1). Their basic features are described here in geographical order along the Lake Ontario coastline from southwest to north east.

Blind Sodus Bay – This is the second deepest of the eight embayments, with a watershed and volume intermediate in size (Table 1.1a). The watershed is 37% covered in agriculture, and there is a moderate community of permanent residences and summer homes along its shoreline so that nutrient loading of both N and P are intermediate relative to the other embayments in this study. Mean seasonal water-column TP is second highest of the embayments, mean TN is intermediate, and it has the second lowest TN:TP ratio (Table 1.1b). The fish community is dominated by piscivores, with the highest piscivore biomass and the third lowest planktivore biomass of the eight systems (Table 1.1c). Blind Sodus B. is connected to Lake Ontario by a shallow (< 1 m deep) sandy channel that is dredged annually at the beginning of the summer and then naturally fills in over the course of the winter.

Little Sodus Bay – The deepest of the embayments (z_{max} 11 m), Little Sodus B also has the second largest volume (Table 1.1a). This system has a long (550 m), 3 m deep, permanent man-made channel, dredged and maintained year-round, between extensive seawalls that connect it to Lake Ontario. The embayment has a very small watershed, with little agricultural influence, and correspondingly low nutrient loading through its single small tributary, although it is surrounded by permanent residences and summer cottages. The embayment itself had a high seasonal mean water column TP for 2002 (3rd highest), but the lowest TN value, which gave it the lowest mean seasonal TN:TP ratio of the eight embayments (Table 1.1b). Both zooplanktivorous and piscivorous fish densities were intermediate compared with the other embayments (Table 1.1c).

Sterling Pond – This is a medium-sized but shallow embayment (Table 1.1a) connected to Lake Ontario by a well-maintained, 3 m deep, permanent channel. It has a relatively large tributary (Sterling Creek) draining the third largest watershed of the eight embayments. This watershed is the most highly agriculture-dominated of the eight embayments (43%), there are no immediately adjacent houses (though it is located within a state campground), and nutrient loading is high for both N and P (Table 1.1b). Nutrient levels were high in Sterling Pond in 2002, with the highest mean water column TP and second highest TN values of the eight embayments, which combined resulted in a relatively low average TN:TP ratio. Sterling Pond contained extensive beds of rooted macrophytes, with the highest submersed-vegetation to open-water habitat ratio of the eight embayments. It supported both large piscivorous and planktivorous fish communities (Table 1.1c).

Juniper Pond – This embayment has the smallest volume, depth (z_{max} 3 m), and watershed size of the eight embayments (Table 1.1a). It also has the weakest

connectivity with L. Ontario: it is separated from the lake by a high coarse gravel and sand bar through which embayment water percolates, keeping the water level in the embayment similar to that of the lake. Its watershed is second highest in terms of percent agriculture but has the smallest total area as it is fed largely by ground water, resulting in the lowest N and P loads of the eight systems (Table 1.1b). There are no houses along its shoreline. Mean seasonal water column TN concentration is intermediate, while TP is the lowest of the other embayments. This system has the third highest ratio of area in rooted vegetation to area of open water, but supports the lowest total fish biomass of the eight embayments (Table 1.1c).

South Sandy Pond – This pond has the second greatest depth and volume of the eight embayments, but the third smallest watershed (Table 1.1a). It has an indirect connection to L. Ontario through a channel to North Sandy P., which, in turn, has a permanent natural connection to the larger lake. Otherwise South Sandy P. is permanently cut off from L. Ontario by a wide, extensively vegetated sand bar. The pond receives an intermediate nutrient load relative to the other embayments from a small watershed that is 29% agricultural land. The pond has permanent residences and summer cottages on two sides, but nevertheless had mean seasonal water column TN and TP values that were the third lowest relative to the others, yielding the third highest TN:TP ratio (Table 1.1b). The system held the highest planktivorous fish biomass, and an intermediate piscivore biomass compared with the other embayments (Table 1.1c).

North Sandy Pond – The embayment with the largest volume of the eight embayments, it is fed by multiple tributaries draining the second largest watershed (Table 1.1a). As mentioned above, this embayment is connected to L. Ontario by a

large, natural and dynamic opening in the sand bar that separates most of the embayment from the lake. Although the watershed supports the third lowest amount of agriculture by area, the nutrient load was relatively high for both N (second highest) and P (third highest), likely due to the relatively high density of permanent residences and summer cottages along or close to the shoreline (Table 1.1b). However, because these loads entered a large water body, well connected to L. Ontario, mean annual water column TN and TP values were both relatively low. North Sandy P. supports the largest abundance of planktivorous fish by biomass of the eight systems, and the second smallest piscivorous fish biomass (Table 1.1c).

South Colwell Pond – This pond is shallow, and is the third smallest embayment by volume (Table 1.1a). It also has the second smallest watershed and second smallest percentage of agriculture (19%). It has no houses near its shoreline. A natural channel connecting the embayment to Lake Ontario is variable in both size and depth, but is generally weak. Nutrient loads from the watershed are low, while mean seasonal water-column TN and TP concentrations were intermediate compared with the other systems (Table 1.1b), as were the abundances of both planktivorous and piscivorous fish (Table 1.1c). South Colwell P. contained large amounts of rooted macrophytes, with a large submersed-vegetation to open-water area ratio, second only to Sterling P.

Floodwood Pond – With an extensive tributary system, Floodwood P. has the largest watershed of the eight embayments by over a factor of ten, with 37% in agriculture and no houses directly along the shoreline, which is predominantly marsh (Table 1.1a). This contrasts with this embayment's relatively small volume (larger only than Juniper P.). It also has a large and permanent natural connection to L. Ontario. In essence this embayment is a wide reach in Floodwood Creek before it enters the lake.

Nutrient loading was highest in this system for both N and P compared with the other embayments, however while mean seasonal TN concentrations were highest in Floodwood P., TP values fell in the middle range relative to the other systems, leading to the highest TN:TP ratio overall (Table 1.1b). Piscivorous fish were in relatively low abundance, while planktivorous fish populations were second highest in total biomass of the embayments (Table 1.1c).

Water retention time gradient

The eight embayments encompass a range of volume, watershed size, and extent of connectivity with L. Ontario, which together determine water retention time. WRT was estimated using passive chemical tracer methodology (C.T. Driscoll and X. Chen personal communication) which allowed us to rank embayments on a relative scale from lowest (rank = 1) to highest (rank = 8) WRT (Table 1.2). While these values are reasonably applicable to a plankton "particle" in most of the embayments, physical barriers such as sand or gravel bars and dense macrophyte beds restrict the movement of plankton in ways that they do not for dissolved chemical tracers. As a result, we modified the original relative WRT ranks as follows. For Juniper P., which has no direct connection to L. Ontario and no tributary flow, WRT calculated from chemical-tracer data must severely underestimate how long plankton remain in the embayment (since there is no clear path for flow of plankton particles between the two systems, unlike the other seven embayments). We designate this embayment to have the highest WRT for plankton, moving its rank from 6 to 8. The other embayment with a WRT rank that we adjusted is Little Sodus Bay. Although there is little watershed drainage through this system, its substantial channel connection to Lake Ontario provides a different avenue for the exchange of water and plankton. Rueda and Cowen (2005) and Doyle-Morin et al. (Chapter 2) have shown that major

Table 1.2 Original (X. Chen, personal communication) and derived water residence time (WRT) data and ranks for eight L. Ontario embayments

	Original WRT Estimates (days)	Original WRT Rank	Revised WRT Rank	WRT Category
Blind Sodus B.	47	4	5	Medium-High
Little Sodus B.	56	5	4	Medium-Low
Sterling P.	1	2	2	Low
Juniper P.	62	6	8	High
South Sandy P.	148	8	7	High
North Sandy P.	35	3	3	Medium-Low
South Colwell P.	90	7	6	Medium-High
Floodwood P.	0.1	1	1	Low

upwelling events in L. Ontario, including one in 2002 between 28 Aug. and 10 Sept., result in exchange flow of cold L. Ontario water flowing in through the channel and forcing warm embayment surface water out to the lake. Other embayments must also experience exchange flow under these conditions but the extent of impact is less because their connections to the lake are smaller, or macrophyte beds restrict flow. To account for this kind of reduction in WRT, we moved Little Sodus B. from a rank of 5 to 4. Finally, we retained the position of Sterling P. in the ranking even though its high macrophyte density in summer and autumn apparently decouples plankton dynamics from mean WRT by in effect channelizing the substantial stream flow across the embayment while sheltering a large fraction of the embayment volume from high water exchange. We do not have an easy way of determining the logical placement of this embayment along our WRT gradient, so instead of moving Sterling P. in our ranking, we note in our statistical analyses how removing it as an outlier greatly improves some relationships. Because the WRT rank is qualitative and probably changes seasonally, for ANOVA analyses we reduced the number of rank categories from 8 (the number of embayments) to 4 with two embayments in each rank.

Sample collection

Samples were collected weekly at a central site in each of the eight embayments from 8 May 2002 through 8 October 2002. Temperature and dissolved oxygen profiles were recorded at half-meter to one-meter intervals throughout the water column at each site using standard equipment (Yellow Springs Instruments Model 58). Replicated phytoplankton samples were collected using a tube sampler that integrated the entire water column, and preserved in 1% Lugol's solution. Samples were settled for at least 24 h and counted at 400× with Wild M40 inverted

microscope (Lund et al. 1958). Additional counts were made at 100× to estimate abundances of larger or rarer forms. Phytoplankton densities were expressed as individuals mL^{-1} or converted to biovolume (μm^3 mL^{-1}) based on cell dimensions (Wetzel and Likens 2000). Zooplankton (also obtained in replicate) were collected by diagonal tow using a Clarke Bumpus quantitative sampler fitted with a 75-μm-mesh net and preserved using 70% ethanol. Individuals were identified to species, measured with an eyepiece micrometer, and counted using an Olympus SZH10 dissecting microscope. Biomasses were calculated using length-weight regression from Bottrell et al. (1976).

Data analysis

Because WRT values are expressed as relative ranks, the relationships between plankton variables and WRT were assessed using a Spearman's Rank Correlation. All numeric correlations used Pearson's Correlation Coefficient. Differences among embayments were assessed using one-way ANOVA, with Tukey HSD-adjusted α-values for individual comparisons. All error estimates reported are ± 1 standard error. Statistical analyses were carried out using Minitab, version 15.1 (2007) and SPSS, version 16.0 (2007). Because it was only possible to sample eight embayments as intensively as we did, and because there is considerable variability in these data, the power to detect statistical trends is limited. For this reason, we have chosen to use $\alpha = 0.1$ as our cutoff for statistical significance.

For many of the analyses, plankton taxa were combined into functional groupings. Phytoplankton edibility was determined by both size and known physiological or morphological defenses; phytoplankton that were greater than 30 μm in cell size or colony dimension, those that had spines or gelatinous sheaths, and those known, at least at times, to produce toxins or to have reduced nutritional value were

categorized as "inedible" (Porter 1973, Vanni and Lampert 1992). All other taxa were placed in the "edible" category, including most small Chlorophyta, Chrysophyta, and Cryptophyta. Grazers were categorized based on literature information on feeding selectivity and mode (filtering or grasping), and adult body size. Large, nonselective filter feeders like *Daphnia, Diaphanasoma, Holopedium,* and *Ceriodaphnia* were included in the "unselective grazer" category, while smaller, more selective cladocerans like *Bosmina, Eubosmina,* and *Chydorus* species comprised the "selective cladoceran" category. Rotifers and the selective cladocerans comprised the high r_{max} species category, while the low r_{max} species category contained the unselective cladocerans and copepods.

To assess the extent to which internal processes drive an embayment's plankton dynamics, we evaluated their fit to the stereotypical seasonal pattern for temperate zone lakes of moderate to high productivity, described by the Plankton Ecology Group (PEG) model (Sommer et al. 1986). Five phases of the PEG dynamics were identified (Fig. 1.3), and a quantifiable index for each was devised. Each index had a range of 0 to 1 with the embayment having the poorest fit to PEG expectation assigned a value of 0 and that with the best fit given a value of 1. Other embayments received fractional values that represented where they lay between the extremes. The PEG phases chosen are as follows.

1) All embayment systems are expected to have a spring edible phytoplankton bloom, however only the higher WRT systems are expected to show a strong coupling between the termination of this bloom and increasing *Daphnia* density as occurs during the clear water phase (CWP). Thus, the strength of spring crash of edible phytoplankton was determined by calculating the maximum range of phytoplankton biovolumes during a period of two or more consecutive weeks of positive edible algae growth in May and early June.

2) The increase in *Daphnia* biomass that accompanied the CWP was made into an index by calculating the fraction of the total zooplankton biomass comprised of *Daphnia* on the date of lowest biovolume of edible phytoplankton in late May or June (as determined in (1)).
3) The N-fixing cyanobacteria maximum was used as a measure of nutrient limitation expected in an enriched, highly coupled system. The index uses the highest biovolume of these taxa during a period of two or more consecutive weeks of positive cyanobacterial growth rates in July and August.
4) Herbivorous copepods with an ability to avoid consumption of cyanobacteria are expected to be abundant in late summer if and when these phytoplankton taxa are abundant. Our index for this period is the fraction of the total zooplankton biomass comprised of copepods on the date of highest N-fixing cyanobacterial biovolume in June and July.
5) The fall bloom of edible phytoplankton was used as a measure of phytoplankton response to fall mixing and release from nutrient limitation. This index was a function of the highest biovolume of taxa in the edible category during September and October.

Results

External forcing versus internal dynamics

We first explored the hypothesis that embayments with low WRT should have plankton dynamics generally synchronized by external forcing (high or low flow events), while the plankton in high WTR embayments should tend to show patterns consistent with strong community interactions. The simplest test was to look for relationships among the abundances of major functional groups across sampling dates for the entire study period in 2002 (e.g. Fig. 1.4). We regressed various combinations

Figure 1.4 2002 phytoplankton and zooplankton community dynamics in Blind Sodus B. (a), Little Sodus B. (b), Sterling P. (c), Juniper P. (d), South Sandy P. (e), North Sandy P. (f), South Colwell P. (g), and Floodwood P. (h). Error bars represent +/- 1 s.e.

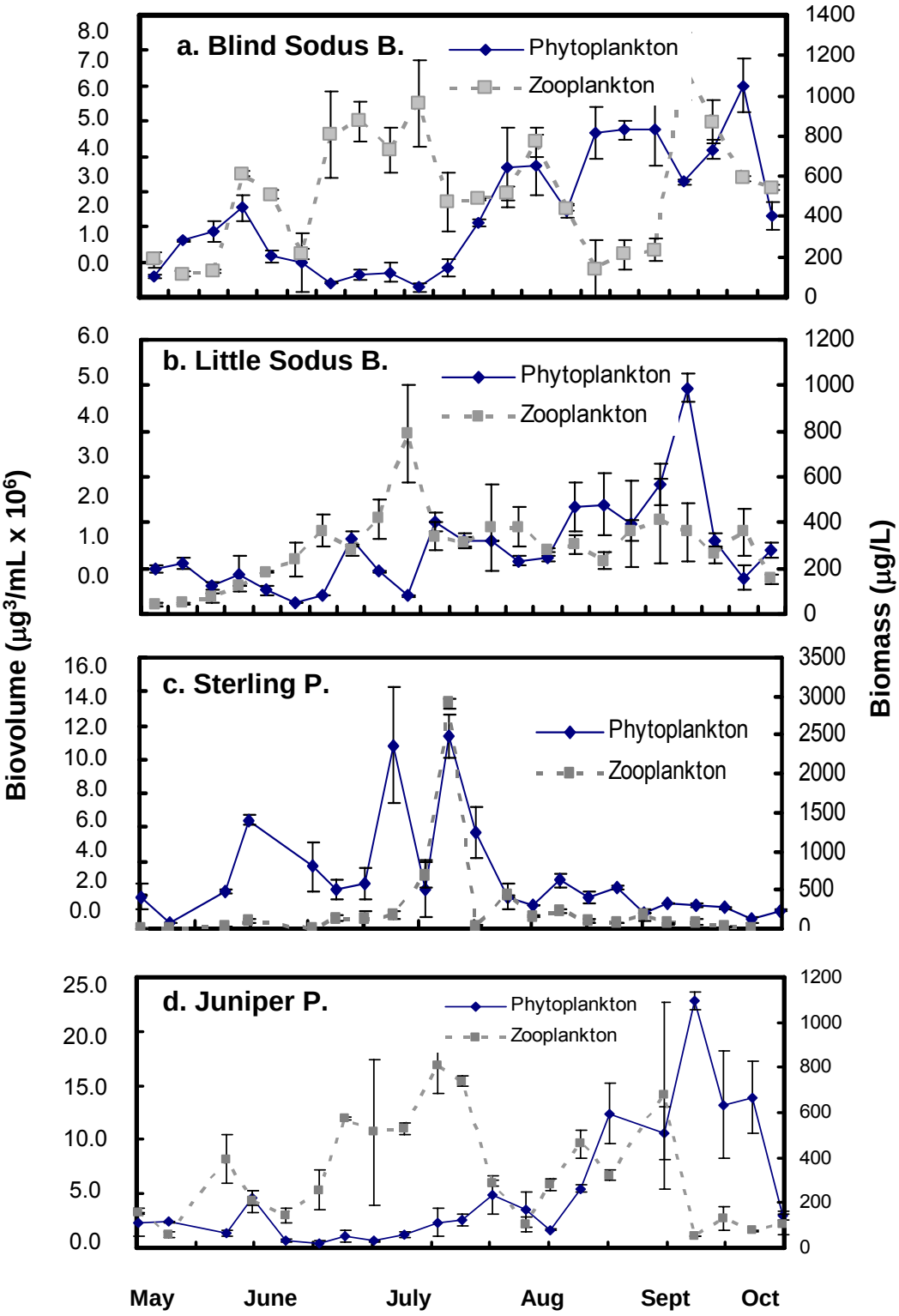
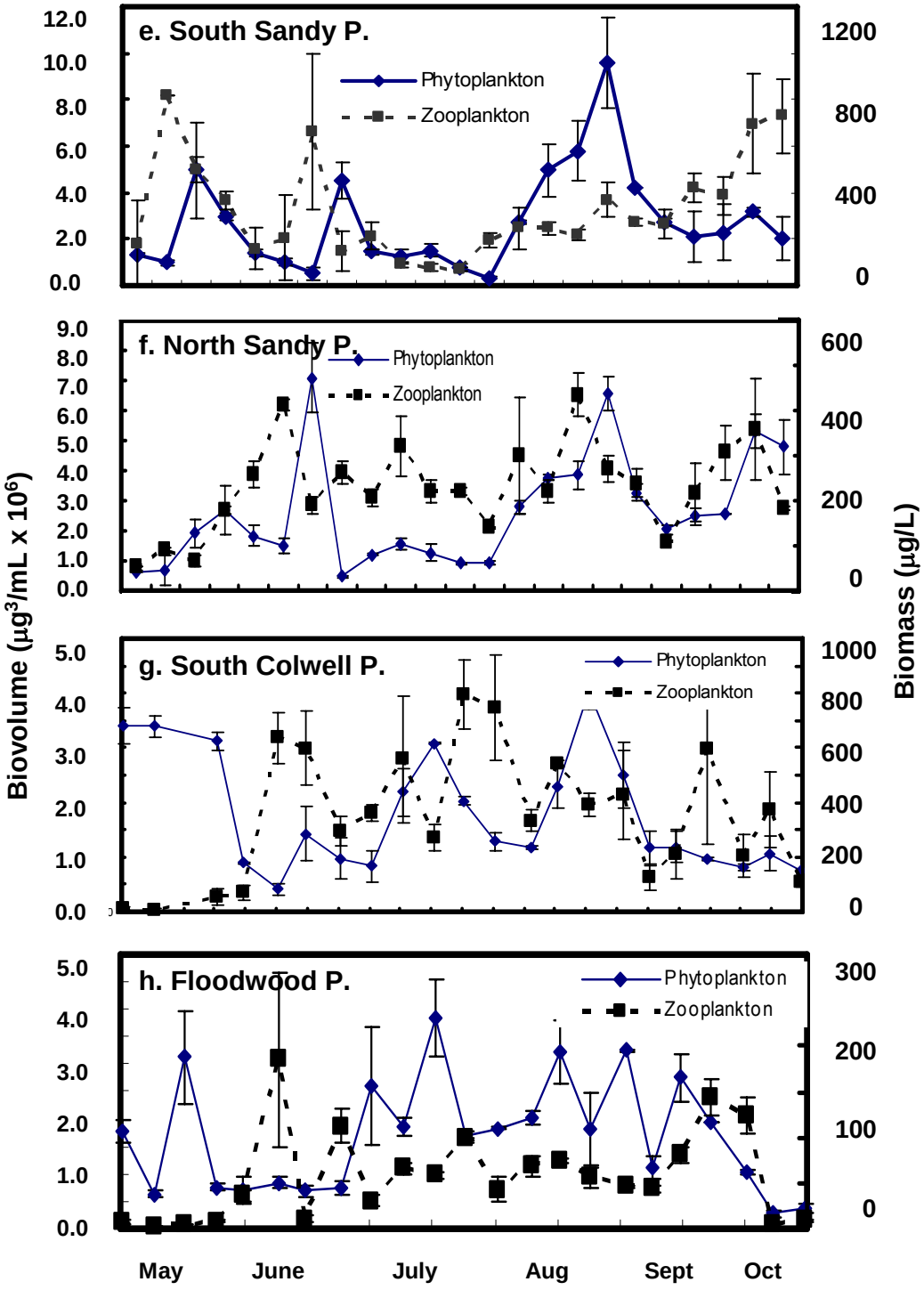

a. Blind Sodus B.
Phytoplankton
Zooplankton
b. Little Sodus B.
Phytoplankton
Zooplankton
c. Sterling P.
Phytoplankton
Zooplankton
d. Juniper P.
Phytoplankton
Zooplankton
Biovolume (µg³/mL x 10⁶)
Biomass (µg/L)
May
June
July
Aug
Sept
Oct

Figure 1.4 continued



of phytoplankton biovolume and zooplankton biomass, from individual embayments, against each other. No significant patterns (negative or positive) were found in any comparison, in any embayment, for likely competitive relationships between phytoplankton functional groups, or between zooplankton functional groups. Similarly, no potential consumer-resource relationships (either monotonic or oscillatory limit cycles) such as might have been expected between total zooplankton densities and total phytoplankton densities were found, even when the zooplankton dynamics were lagged behind the phytoplankton by a week (i.e., roughly the generation time of the major grazing cladocerans during much of the summer).

One possible explanation for not finding any relationships among the abundances of different functional groups, is that plankton dynamics are seasonally driven so that even when biological coupling is strong, the nature of those ecological interactions changes from one time of year to the next and analysis of all dates in a single statistical test is unlikely to show any relationships. When we divided the seasonal data for each embayment and scored them for consistency with major periods described in the PEG Model (Sommer et al. 1986), as described in Methods, we see a pattern emerge. Although there is no discernable relationship between mean PEG index and WRT when all eight embayments are included, the relationship is significant once Sterling P. is dropped from the analysis (for reasons given previously) (Fig. 1.3; Spearman Rank $\rho = 2.218$; $p = 0.077$). Blind Sodus B. had the highest mean PEG index, exhibiting moderate to strong consistency for all five phases during the 2002 growing season, as would be expected for an embayment where external forcing is weak compared with the strength of internal self-organization. This was the case for Blind Sodus B. even though it was scored as intermediate in WRT. At the extreme low end of WRT, Floodwood P. had the weakest consistency with PEG dynamics, with only a late-summer copepod increase fitting the reference pattern, as would be

expected of an externally forced system. Note that Sterling P. was the embayment that ranked second in consistency with PEG dynamics, and although this is not expected based on our WRT ranking, it likely resulted from the effects of macrophytes that make Sterling P. an outlier.

Plankton assemblage matching to water retention time

When compared with ranked WRT, both ranked mean phytoplankton biovolume and ranked mean zooplankton biomass over the entire sampling period showed positive trends, with greater densities in embayments with longer WRTs (Fig. 1.5; Spearman Rank phytoplankton $\rho = 0.405$; $p = 0.320$; zooplankton $\rho = 0.738$; $p = 0.037$). This is the case for phytoplankton biovolume only when Sterling P. is removed as an outlier (Spearman Rank $\rho = 0.69$; $p = 0.094$), which in addition to the explanation in Methods, is necessary because the phytoplankton samples unavoidably contained many epiphytic taxa presumably knocked off of macrophytes during sampling. When the phytoplankton data are broken into the "edible" portion of the community (the smaller, faster growing, typically high r_{max} species) and the "inedible" part (the larger, more highly defended species with lower r_{max} values), the relationships trend in opposite directions (Fig. 1.6; Spearman Rank edible $\rho = -0.524$; $p = 0.183$; inedible $\rho = 0.548$; $p = 0.160$) with the edible fraction becoming less abundant and the inedible fraction increasing with lengthening WRT, as grazer density increases (c.f., Fig. 1.5b). These opposing trends are statistically significant when combined as a measure of percent of phytoplankton biovolume that was edible (Fig. 1.6c; Spearman Rank $\rho = -0.69$; $p = 0.058$).

Not only did phytoplankton composition depend upon WRT, but overall phytoplankton diversity (Simpsons Ds) decreased in value as WRT lengthened (Fig. 1.7; Spearman Rank $\rho = -0.786$; $p = 0.021$), suggesting that the same environmental

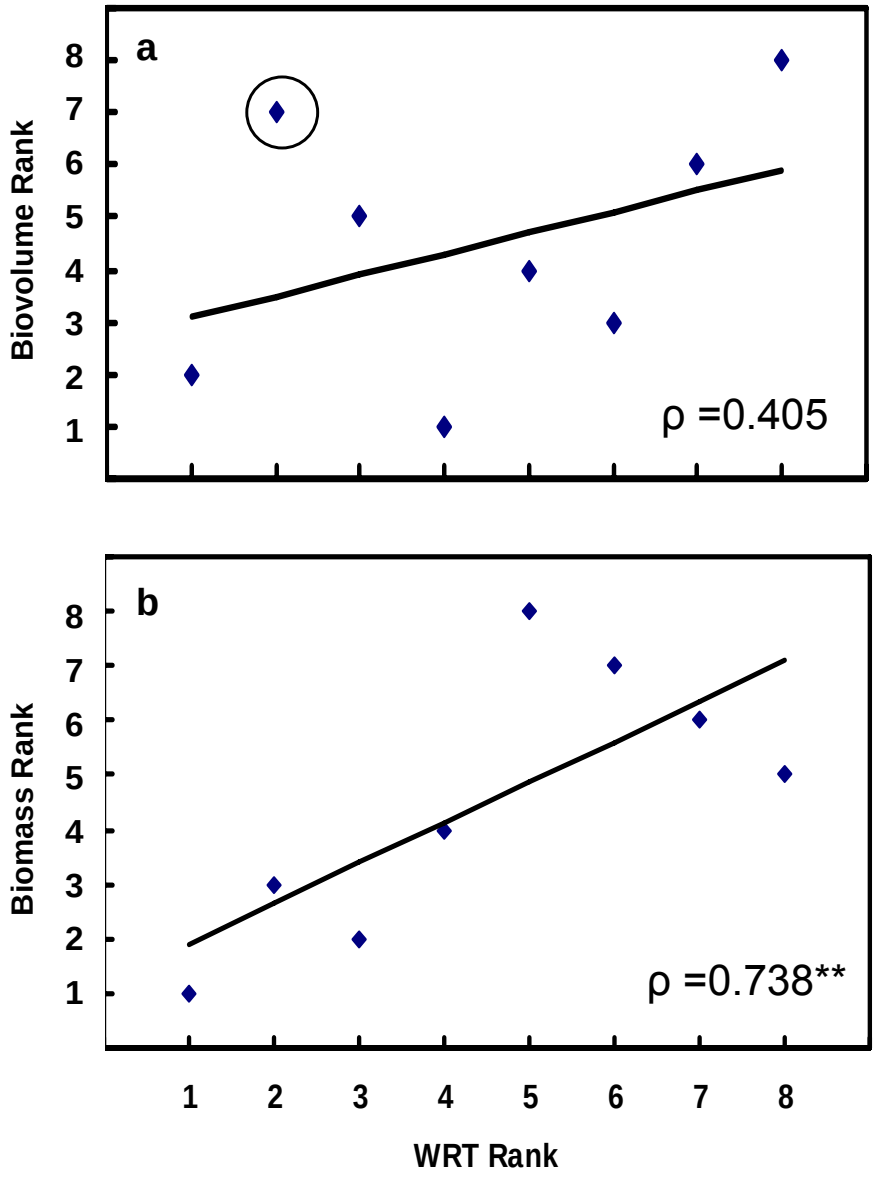


Figure 1.5 Embayment average 2002 phytoplankton (a) and zooplankton (b) values plotted against water residence time (WRT) ranking. Spearman's ρ values are listed. Asterisks indicate significant effects at the $p \leq 0.10$ level (*) or $p < 0.05$ level (**). The Sterling P. phytoplankton outlier is circled. ρ =0.69* when outlier is removed.

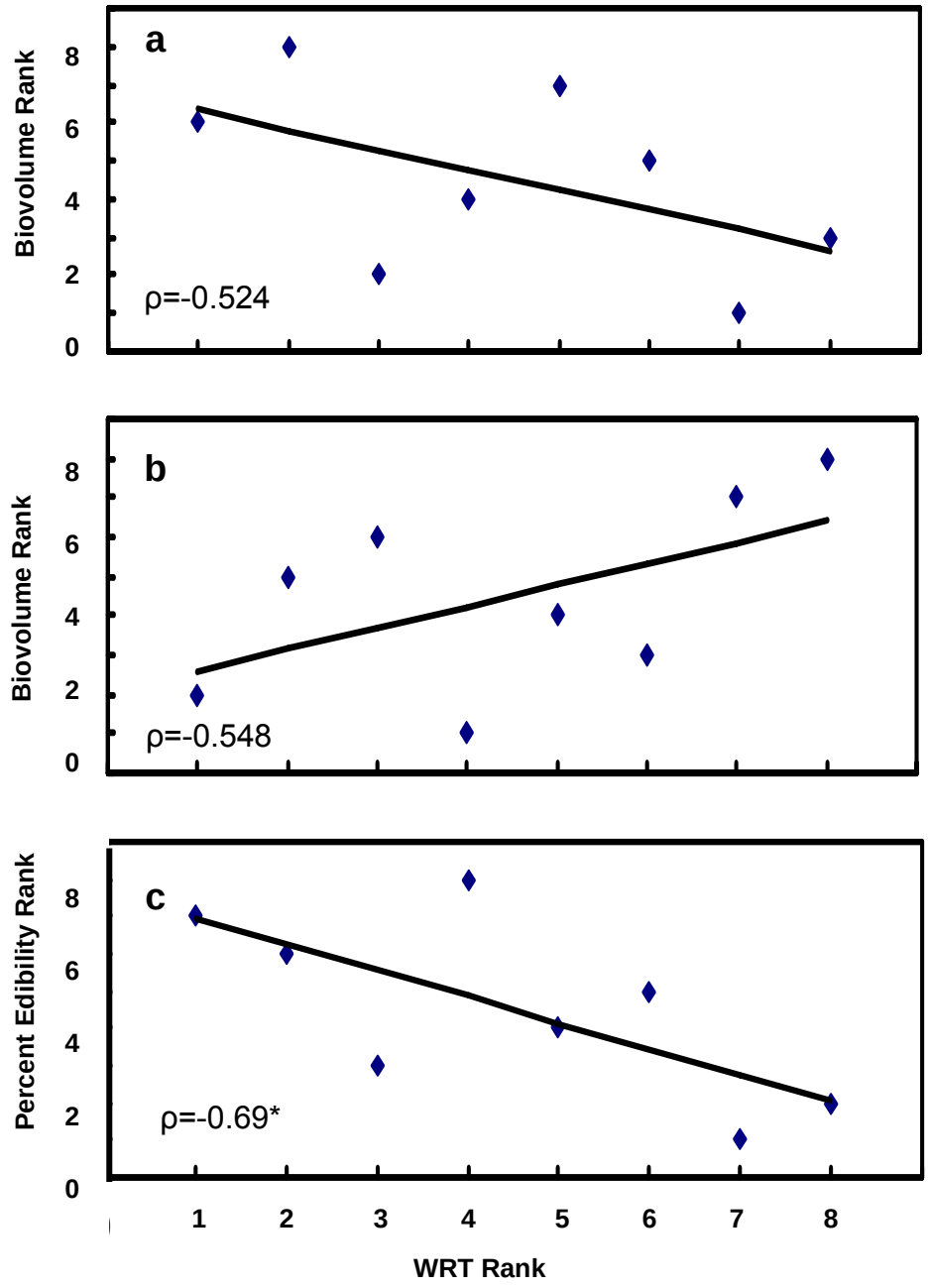


Figure 1.6 Embayment average edible (a) and inedible (b) phytoplankton biovolume values, as well as % phytoplankton edibility (c), plotted against water residence time (WRT) ranking. Spearman's ρ values are listed. An asterisk indicates significant effects at the $p \leq 0.10$ level.

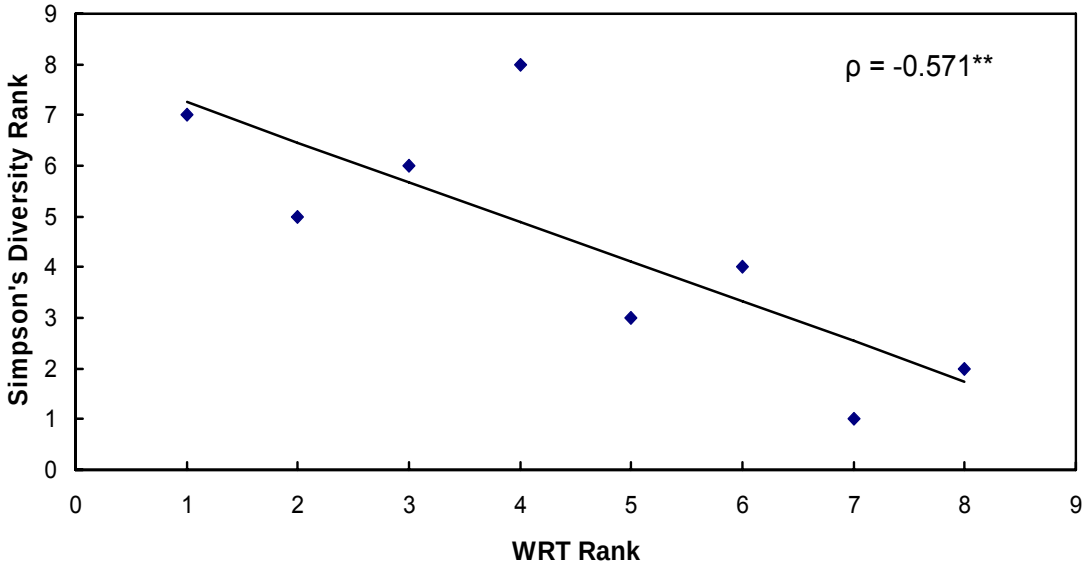


Figure 1.7 Simpson's phytoplankton diversity versus water residence time ranking (low=1). Ds values range from 0.81 - 0.91.

conditions that are conducive to slow growing, well defended phytoplankton groups also resulted in assemblages dominated by only a few taxa.

The biomass abundance of slow-growing, low r_{max} zooplankton taxa was significantly positively related to increasing WRT (Fig. 1.8a; Spearman Rank ρ = 0.786; p = 0.021). Animals that cannot increase rapidly in numbers do best in embayments that do not wash them out at a high rate. In contrast, fast-growing, high r_{max} zooplankton taxa had no monotonic relationship with WRT (Fig. 1.8b; Spearman Rank ρ = -0.119; p = 0.779), but instead exhibit maximum biomass abundance at intermediate WRT (Fig. 1.9). When the low r_{max} group is broken down into two taxonomic subcategories, adult copepods, which are slow growing, show a strong positive correlation of biomass with WRT (Fig. 1.10a; Spearman Rank ρ = 0.619 ; p = 0.102). The *Daphnia* pattern does not hold when the eight embayments are ranked for WRT separately because *Daphnia* was scarce in Juniper P., which had the highest WRT rank, while another slow-growing group, calanoid copepods, dominated (Fig. 1.10b; Spearman Rank ρ = 0.190 ; p = 0.651). The highest r_{max} zooplankton group, the rotifers, occurred in greatest abundance in the medium-low WRT embayment systems (ANOVA, F = 14.141, p = 0.014), while small cladocerans, the next fastest reproducing group (i.e., *Bosmina* sp. and *Chydorus* sp.), showed a significantly higher abundance in the medium-high WRT systems relative to the others (Fig. 1.9; ANOVA, F = 4.450, p = 0.092). Unlike the phytoplankton, there was no discernable pattern between zooplankton diversity and WRT.

Discussion

Our analysis of the eight embayments along the shore of Lake Ontario shows that both plankton composition and seasonal dynamics are related to water retention time, though not in a way suggestive of laboratory chemostat dynamics. There were

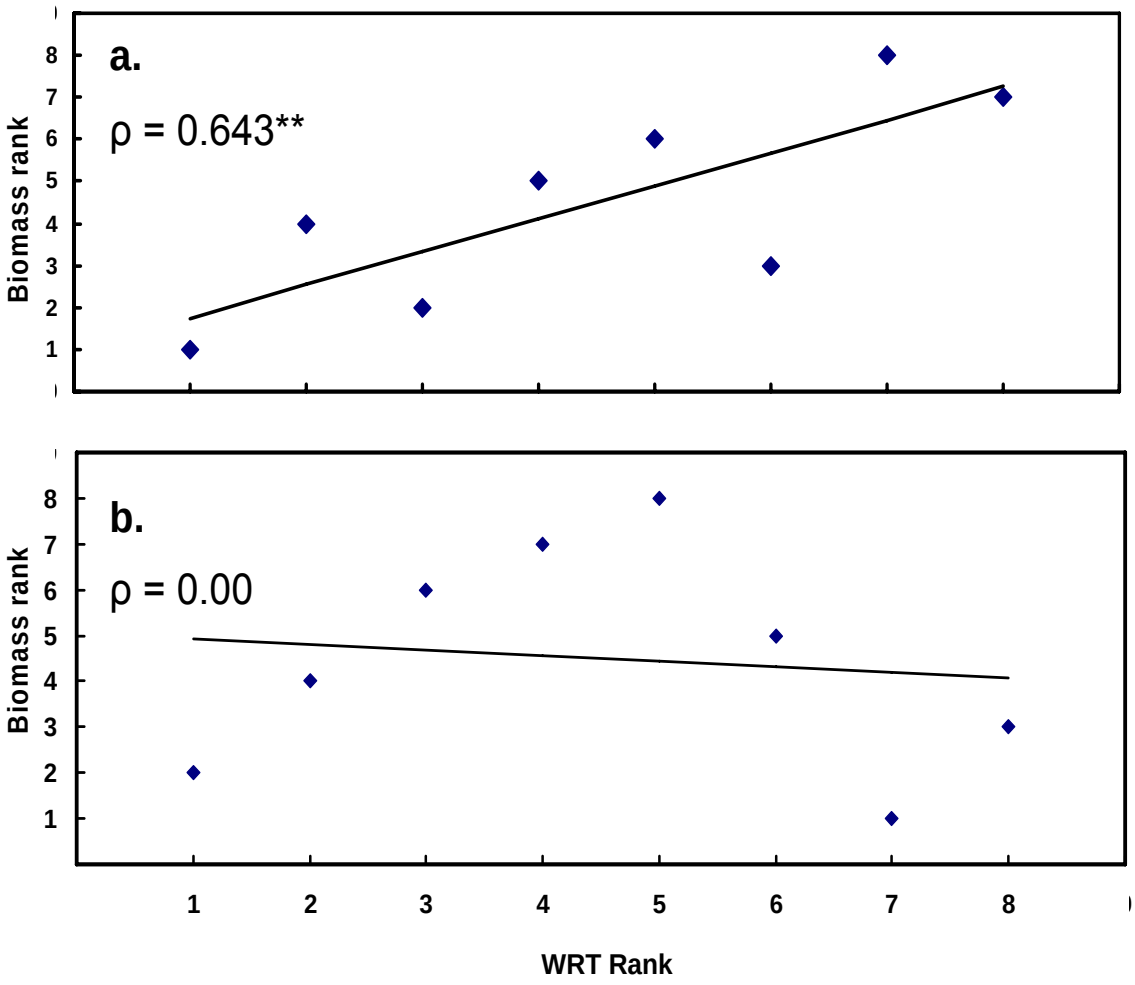


Figure 1.8 Ranked low (a) and high (b) r_{max} zooplankton species biomass versus ranked WRT. Asterisks (**) indicate significant effects at the $p \leq 0.05$ level.

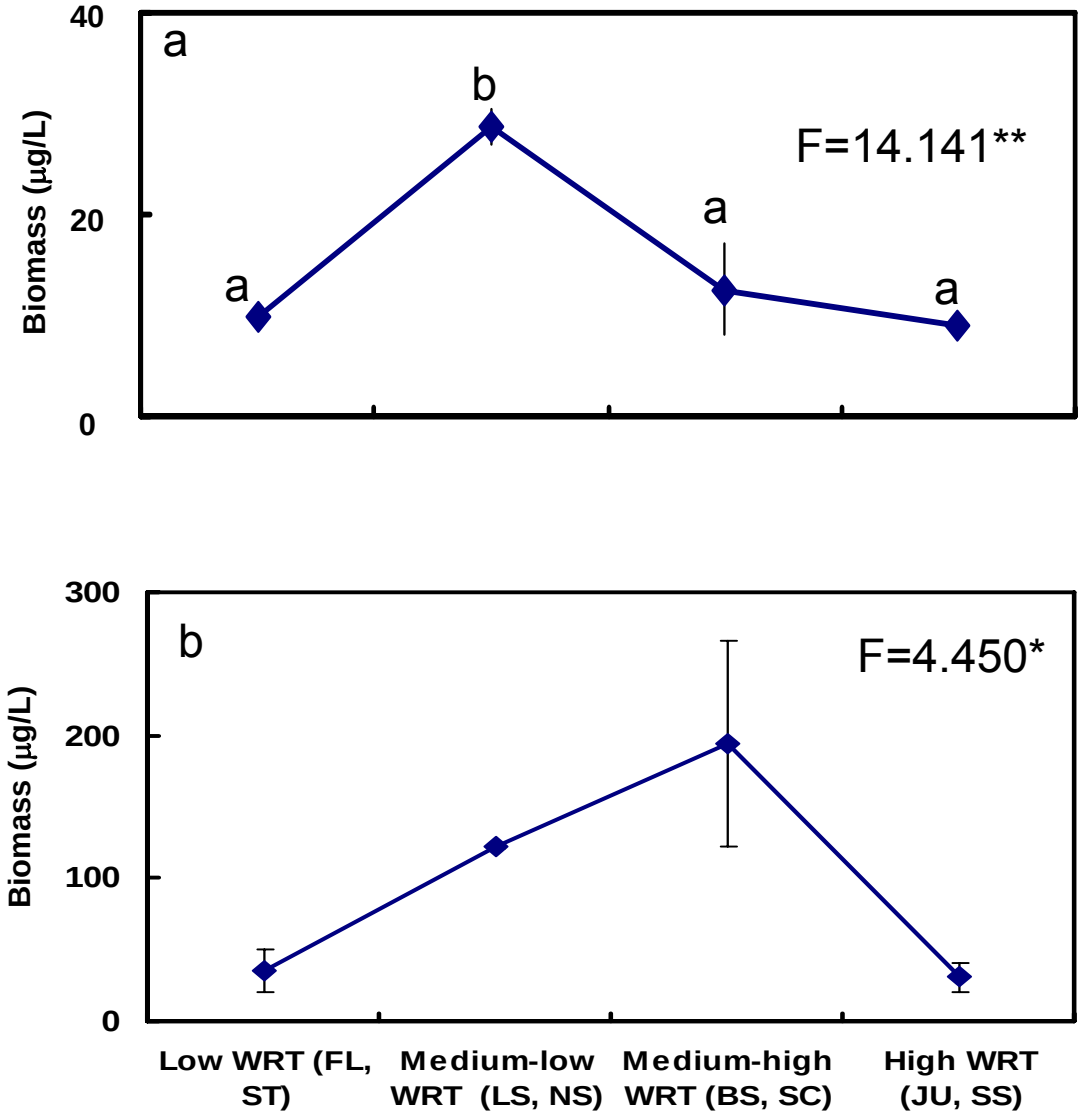


Figure 1.9 Average 2002 rotifer (a) and small selective cladoceran (b) biomass versus WRT groupings. Asterisks indicate significant effects: ** $p \leq 0.05$, * $p \leq 0.10$. Letters indicate statistically significant post-hoc differences.

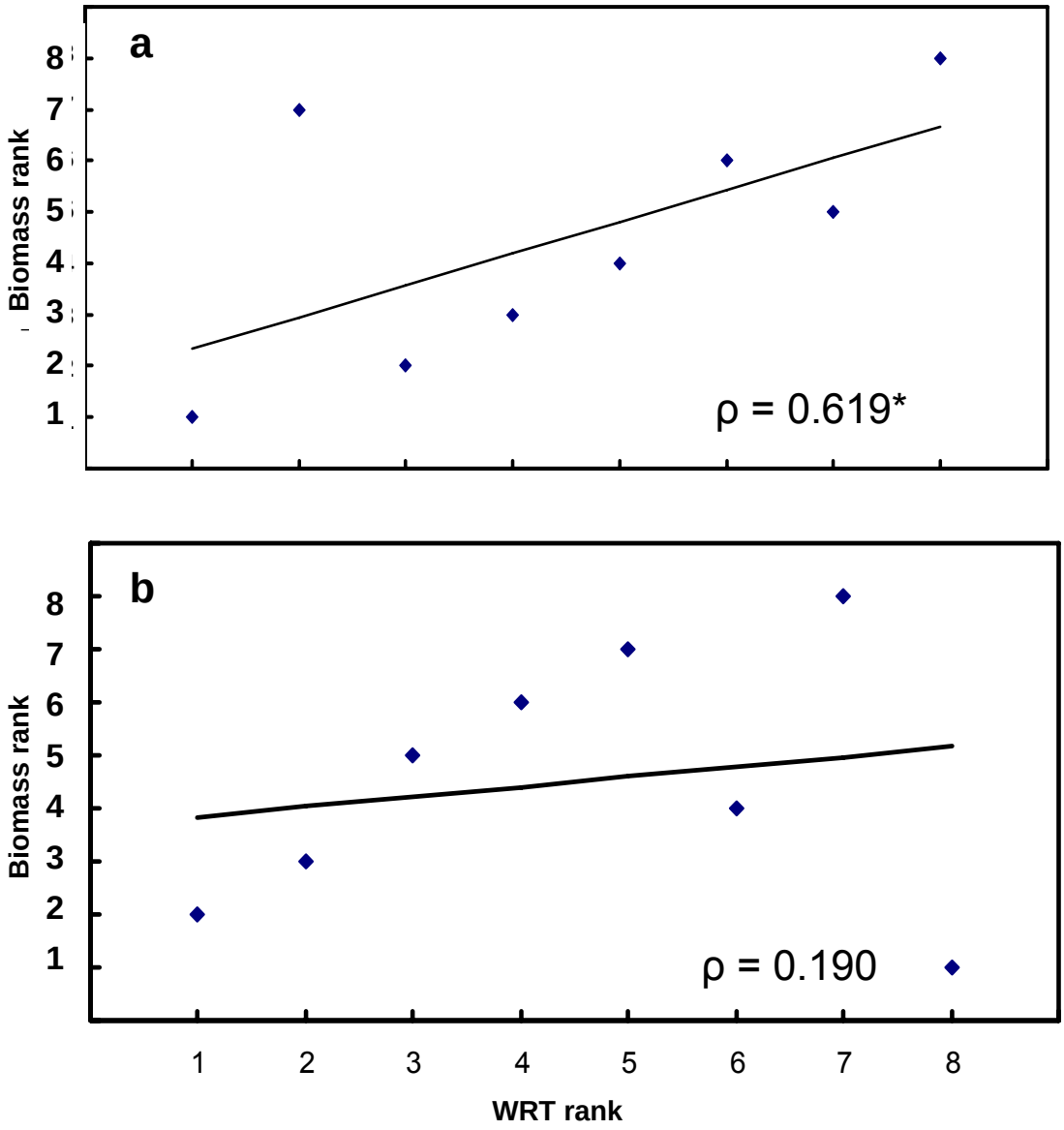


Figure 1.10 Average adult copepodid (a) and *Daphnia* (b) biomass vs WRT. Asterisks indicate significant effects: * $p \leq 0.10$.

few of the positive or negative correlations within or between phytoplankton and zooplankton functional groups predicted based on this simple explanation. There was no evidence of a relationship between the strength of community interactions between functional groups and WRT. Instead, we found that the dominant taxa present within each trophic level changed as a function of WRT. Low r_{max} species of both phytoplankton and zooplankton were most abundant in high WRT systems and high r_{max} species dominated in those with low WRT (Figs. 1.6 and 1.8). Nevertheless, once seasonality was considered, we found a significant pattern of increasing consistency between embayment plankton dynamics, stereotypical pelagic processes described by the standard PEG model, and system WRT (Fig. 1.3).

Low WRT systems

There are several potential explanations for why we did not find distinct, strong, positive correlation we predicted in the two lowest WRT systems, Floodwood P. and Sterling P., based on chemostat dynamics. As previously mentioned (see Methods), placing Sterling P. at the low end of the WRT gradient is questionable because of the extensive macrophyte growth that fills this embayment at the primary sampling site, especially in the late summer. Additional research (King 2006) has shown that these macrophytes play a role in increasing WRT seasonally, creating a physical barrier isolating the plankton from stream flow (see Chapter 2). This would allow quickly-growing phytoplankton to take advantage of the high nutrient loads percolating through this system without being washed out, and may account for the unexpectedly high phytoplankton abundance during the early summer months, before tributary flow waned and increasing macrophyte density started to restrict circulation within the system. This system, however, is also at times an extremely low WRT system (c.a. 0.6 day WRT, King 2006) before macrophytes become dominant, or after

the Sterling P. macrophyte community was mechanically harvested, so giving it a WRT ranking closer to larger less-connected systems would not have been appropriate.

Macrophytes were not the only complicating factor for our low WRT site designations during this sampling season. While both Floodwood P. and Sterling P. appear to be highly connected both to their watersheds and to L. Ontario, physical exchanges with the watershed and lake were not as strong as expected when we studied them during summer 2002; the two main physical drivers, precipitation and wind, were generally low and not sufficient to cause tributary flow or embayment-lake exchange for much of that year. As a result, the low WRT systems may have only had a low WRT at the same time that other embayments are undergoing seasonal temperature-driven spring bloom and fall overturn periods, making it difficult to differentiate these more strongly externally forced systems. In addition, these two systems likely did not represent an extreme of low WRT because both have nearby plankton sources (macrophyte beds and low flow lobe in Sterling P., adjacent wetland in Floodwood P.) that may have contributed to species abundance and diversity.

Nevertheless, both Floodwood and Sterling Ponds did have some of the characteristics expected of embayments at the low end of the WRT gradient, underlying the significant correlations that we did find. Both Floodwood and Sterling P. had relatively low zooplankton biomass, which can likely be attributed to high wash-out rates in Floodwood P. This may also be the case early in the season in Sterling P. before the macrophytes fill in completely, however, it is more likely to have been due to high predation by omnivorous fish (dominated by *Lepomis gibbosus* and small-bodied *Perca flavescens*) which had an extensive refuge (macrophytes) from piscivores (Table 1.1c). This low zooplankton abundance may, in turn, have been an important factor explaining the high phytoplankton density in Sterling P.,

further allowing particularly fast growth of the populations in the higher WRT conditions. As the lowest WRT system, Floodwood P. more consistently fell within the range expected for the variables sampled, with a low biovolume of highly edible phytoplankton, relatively low cyanobacterial density, and a relatively diverse zooplankton community that included the second highest percentage of rotifers (with the fastest zooplankton growth rate) and second lowest percentage of the large grazing crustaceans, like *Daphnia*, which are not expected to do well in low WRT systems (Doyle-Morin, unpublished data; Fig. 1.10b). Floodwood P. was also the system that was the least consistent with the PEG model, only scoring above the minimum for one index: high summer copepod abundance (Fig. 1.3), and even that instance may have resulted from a somewhat anomalous combination of unusually low-flow conditions in mid-summer 2002 and copepod recruitment from the adjacent marsh.

Interestingly, neither Floodwood P. nor Sterling P. had the greatest biomass values for the high r_{max} taxa rotifers and small cladocerans: those occurred in either medium-low WRT systems (rotifers; Fig. 1.9a) or medium-high WRT systems (small cladocerans; Fig. 1.9b). Apparently, even the fastest growing rotifers could not grow fast enough to overcome some effect of high washout. Small cladocerans grow more slowly than rotifers (and may be stronger competitors), and thus attained maximum density in the medium-high WRT embayments, while in the high WRT embayments, competition with the largest grazers may limit the growth of both groups.

High WRT systems

The high WRT systems, South Sandy P. and Juniper P., more clearly represent an extreme end of the WRT gradient. They both had high plankton abundances, dominated by a small number of low r_{max} taxa. Low diversity, driven by substantial populations of cyanobacteria and abundant large grazing zooplankton (i.e., selectively

feeding calanoid copepods in Juniper P. and *Daphnia* spp. in South Sandy P., see Appendix) likely reduced the strength of any consumer-resource dynamics in these systems. Although we did find some patterns in the plankton indicative of negative consumer-resource relationships between trophic levels, these were not the dominant community dynamics for these two systems. Reciprocal dynamics between edible phytoplankton and large grazing cladocerans occurred in Juniper P. (Fig. A.5), but abundances were so low compared with the much denser cyanobacteria and copepods that they did not contribute detectably to broad trophic dynamic patterns. South Sandy P. pelagic processes appear to be driven from the bottom of the food chain, with the highest N and P loads of the four highest WRT systems (Table 1.1b,c), resulting in high biomasses at each trophic level relative to other embayments, including an additional predatory invertebrate group (*Leptodora kindtii*) not found in substantial abundance in any of the other embayments. Bottom-up forcing by nutrients may be the cause of the muted dynamics between trophic levels in this pond, although there were reciprocal interactions within the trophic levels, such as the competitive dynamics among some of the crustaceans (Fig. A.6).

Intermediate WRT systems

We recorded the strongest consumer-resource coupling between zooplankton and phytoplankton in the intermediate WRT system, Blind Sodus B. This was the only embayment during the 2002 growing season to exhibit all of the five PEG model characteristics we scored (Fig. 1.3). Blind Sodus B. has a food chain that appears to be forced from the top-down, with high abundance of piscivorous fish producing low density of zooplanktivorous fish, which, in turn allowed high cladoceran biomass, intermediate phytoplankton abundance, and high water-column TP (Table 1.1b,c, Table A.1). The phytoplankton and zooplankton communities appear to have

negatively correlated dynamics for much of season, with all of the typical successional dynamics, like the early summer crash in the edible phytoplankton community coinciding with an increase in large grazers like *Daphnia*. Like South Sandy P., we also documented a succession of cladoceran species in this system, with a pattern of reciprocal abundance between the bosminid cladocerans, *B. longirostris* and *E. coregoni*, providing the clearest example (Fig. A.3).

The other intermediate WRT system, Little Sodus B., also appears to follow typical PEG-model lake dynamics. Reciprocal consumer-resource dynamics occurred at the beginning and end of the growing season (Fig. 1.4b), but this was absent in summer. One cause of the mid-summer interruption in consumer-resource dynamics, which also explains an early fall bloom and disappearance of heterocysts from the cyanobacteria community (Fig. A.4), is the occurrence of an upwelling event in L. Ontario that drove exchange flow with the embayment in late August and early September (Chapter 2). Upwelling events are the largest source of water exchange for this embayment (Rueda and Cowen 2005), which is particularly vulnerable to L. Ontario forcing because of the permanent, human-maintained channel connecting the two water bodies.

Conclusions

We did not observe strong positively or negatively correlated seasonal dynamics among functional plankton groups that a simple application of chemostat dynamics predicted for our gradient of low-to-high WRT embayments. Chemostats control three things that are not representative of natural water bodies: (1) identical species throughout the season within each embayment, and (2) identical species among embayments, from one extreme end of the WRT gradient to the other, and (3) controlled and constant external environment and flow of medium. Because these are

demonstrably not the case for the embayment systems, we identified two additional approaches to measuring the relationship between plankton community dynamics and WRT.

Regardless of their connection to the surrounding terrestrial and aquatic habitats, each of these systems is externally forced by seasonal changes in temperature and sunlight that result in a replacement of one species by another in response to the physical, chemical, and biological changes in their environment. The PEG model indices we developed represent an objective means of assessing the prevalence of internally driven dynamics in these systems. The increase in correspondence with the PEG model with increasing WRT (with the removal of Sterling P. as an outlier) suggests that external forcing does disrupt typical plankton dynamics and the greater the water flow rate, the greater the disruption to internal self-organization.

This result is not independent of our observation that community composition also changes in response to WRT: low r_{max} taxa dominate the high WRT systems and the r_{max} of the dominant taxa in each embayment increases as WRT decreases. The prevalence of high r_{max} taxa like rotifers in low WRT embayments and bosminid cladocerans in medium WRT systems demonstrate the important effect of high water flow on community composition. Given that PEG dynamics are in many cases a function of the interactions of low r_{max} species like *Daphnia*, copepods, and cyanobacteria, it makes sense that we find the greatest consistency with PEG dynamics in high WRT embayments where these slowly growing taxa can persist and the least consistency in low WRT embayments.

APPENDIX 1A

SEASON AVERAGES AND COMMUNITY DYNAMICS
FOR INDIVIDUAL EMBAYMENTS

Blind Sodus Bay

Seasonal averages: When averaged over the entire 2002 growing season, Blind Sodus B. supported an intermediate total phytoplankton biovolume compared with the other embayments, with half of the community being edible (Table A.1). Consistent with its low water column N:P, this embayment had the second highest ratio of heterocysts to vegetative cells for N-fixing cyanobacteria in what was a medium-density cyanobacterial community. The zooplankton had the highest average seasonal biomass of the eight embayments, dominated by cladoceran biomass almost two times that of the next largest cladoceran assemblage (South Sandy P.). Both selective and unselective cladocerans were abundant, with *Daphnia* accounting for over 20% of the season's total zooplankton biomass. Species richness was low in both the phytoplankton and zooplankton communities, however because species replaced one another seasonally (particularly within functional groups), evenness was high. While overall phytoplankton diversity levels fell in the middle range, crustacean diversity was relatively high compared with the other embayments.

Community dynamics: The phytoplankton community in Blind Sodus B. began the growing season with a bloom of small edible taxa, including cryptomonads, chrysophytes, and chlorophytes (Fig. A.1a). There was also a small peak of edible phytoplankton in late June, but generally the phytoplankton remained at low

Table A.1 2002 seasonal embayment average phytoplankton (a) and zooplankton (b) data. Diversity measures (c) are also listed.

a) Phytoplankton	Phytoplankton Biovolume ($\mu g/mL \times 10^6$)	Phytoplankton % Edibility	Cyanobacteria Biovolume ($\mu g/mL \times 10^6$)	Heterocyst: Vegetative Cell Ratio
Blind Sodus B.	2.4	52	0.25	0..04
Little Sodus B.	1.5	75	0.38	0.07
Sterling P.	3.0	60	0.48	0.04
Juniper P.	5.4	32	0.64	0.04
South Sandy P.	2.8	31	1.23	0.03
North Sandy P.	2.8	40	0.69	0.02
South Colwell P.	1.8	56	0.52	0.02
Floodwood P.	1.7	69	0.08	0.04

Table A.1 continued

b) Zooplankton	Zooplankton Biomass (μg/L)	Low r_{max} Species Biomass (μg/L)	High r_{max} Species Biomass (μg/L)	% High r_{max} Species Biomass
Blind Sodus B.	524	184	274	52
Little Sodus B.	290	86	153	53
Sterling P.	245	79	60	24
Juniper P.	308	185	49	16
South Sandy P.	328	231	31	9
North Sandy P.	229	24	148	65
South Colwell P.	336	71	139	42
Floodwood P.	57	8	31	54

Table A.1 continued

c) Diversity measures	Phytoplankton Diversity (D_s)	Phytoplankton Richness (# spp)	Crustacean Diversity (Ds)	Crustacean Richness (# spp)
Blind Sodus B.	0.86	58	0.73	15
Little Sodus B.	0.91	63	0.71	16
Sterling P.	0.87	72	0.86	16
Juniper P.	0.81	83	0.91	14
South Sandy P.	0.81	50	0.95	17
North Sandy P.	0.88	59	0.55	20
South Colwell P.	0.87	46	0.83	17
Floodwood P.	0.89	64	0.81	18

Figure A.1 Edible and inedible phytoplankton dynamics in L. Ontario embayments (Blind Sodus B. (a), Little Sodus P. (b), Sterling P. (c), Juniper P. (d), South Sandy P. (e), North Sandy P. (f), South Colwell P. (g), Floodwood P. (h)). Error bars represent +/- 1 s.e.

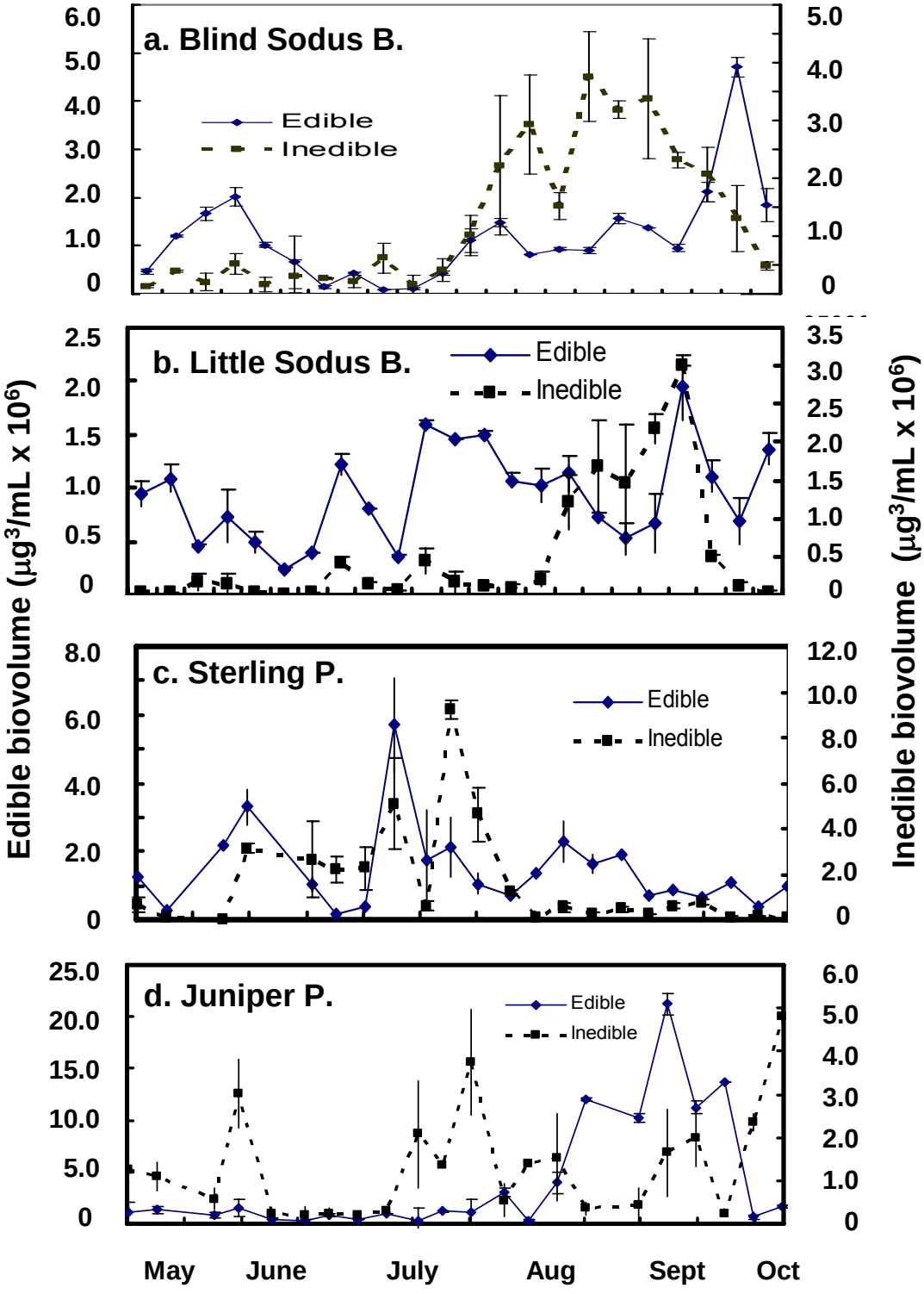
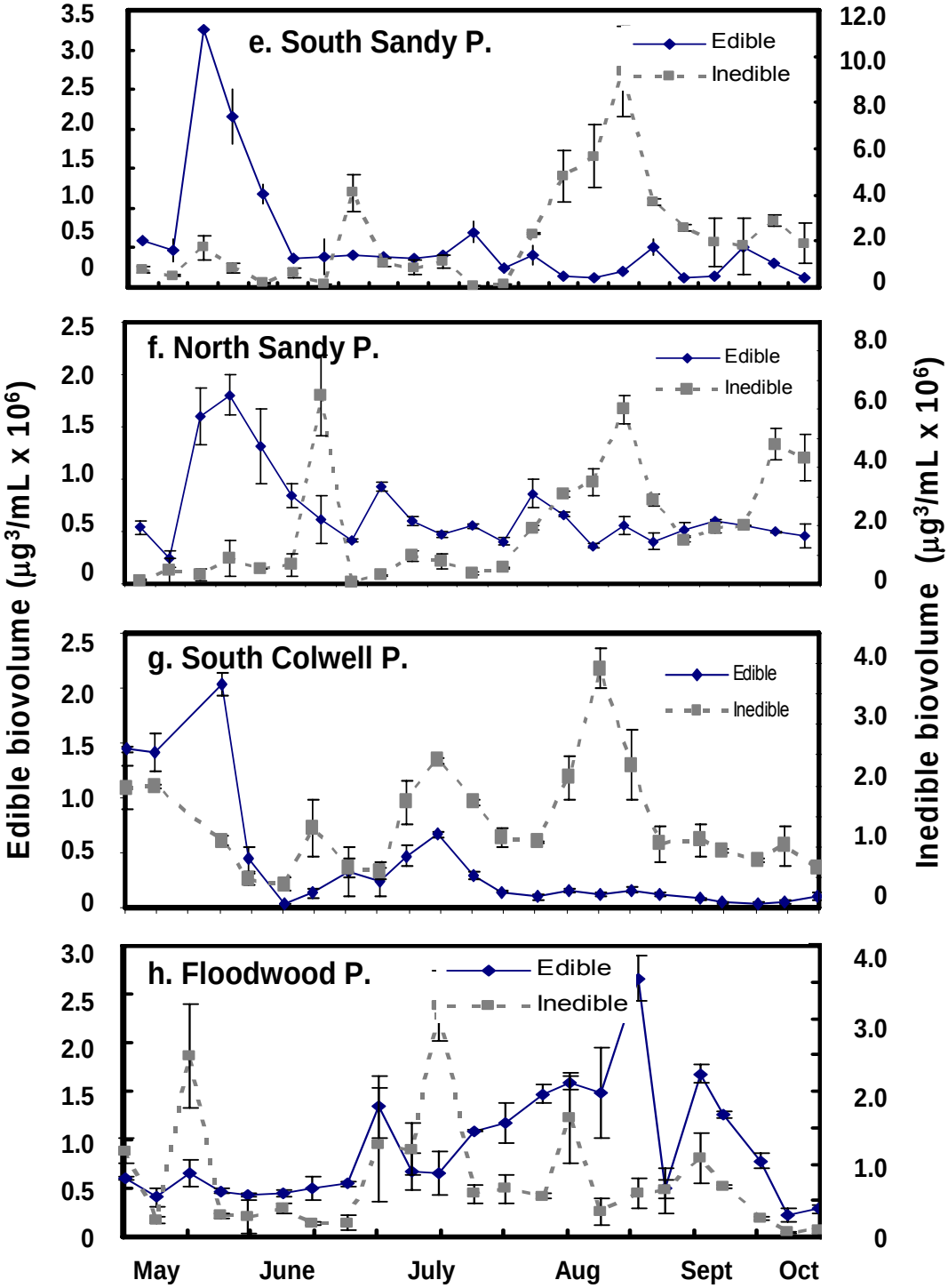

a. Blind Sodus B.
Edible
Inedible
b. Little Sodus B.
Edible
Inedible
c. Sterling P.
Edible
Inedible
d. Juniper P.
Edible
Inedible
Edible biovolume (µg³/mL x 10⁶)
Inedible biovolume (µg³/mL x 10⁶)
May
June
July
Aug
Sept
Oct

Figure A.1 continued



biovolume throughout the summer before both edible and inedible taxa increased in late July. A bloom of large inedible phytoplankton, predominantly comprised of N-fixing *Anabaena* and *Aphanizominon*, lasted from July through September. The season ended with a bloom of diatoms dominated by *Aulacoseira*.

Zooplankton density in Blind Sodus B. started low, before an initial spring peak comprised predominantly of *Bosmina longirostris* (Fig. A.2a, Fig. A.3). This was followed from mid-June to mid-July by a period of high density dominated by *B. longirostris,* cyclopoid copepods, and *Daphnia* spp., peaking in that order (Fig. A.2a). The peak in copepods and *Daphnia* spp. followed the crash in edible phytoplankton, after which these two functional groups (edible phytoplankton and large crustacean grazers) fluctuated oppositely one another (with the exception of a short period in early August) (Fig. 1.4a). Copepods dominated the early August peak before all of the zooplankton declined to biomass levels comparable to those present at the start of spring sampling. A final fall peak in zooplankton was comprised predominantly of *Eubosmina coregoni*, which appeared as the *B. longirostris* population crashed out altogether, finishing a distinct succession of cladocerans through the growing season (Fig. A.3; significant negative correlation between *E. coregoni* and *B. longirostris*, $r = -0.53$, $p \leq 0.01$).

Little Sodus Bay

Seasonal averages: Little Sodus B. had the smallest mean seasonal phytoplankton biovolume with the lowest overall diversity of the eight embayments (Table A.1). Mean percent edibility (75%) was greatest, with cyanobacteria low relative to the other systems, although those present have the highest ratio of heterocysts to vegetative cells (consistent with having the lowest water column N:P). Whereas total

Figure A.2 2002 zooplankton community dynamics in Blind Sodus B. (a), Little Sodus B. (b), Sterling P. (c), Juniper P. (d), South Sandy P. (e), North Sandy P. (f), South Colwell P. (g), and Floodwood P. (h). Error bars represent +/- 1 s.e.

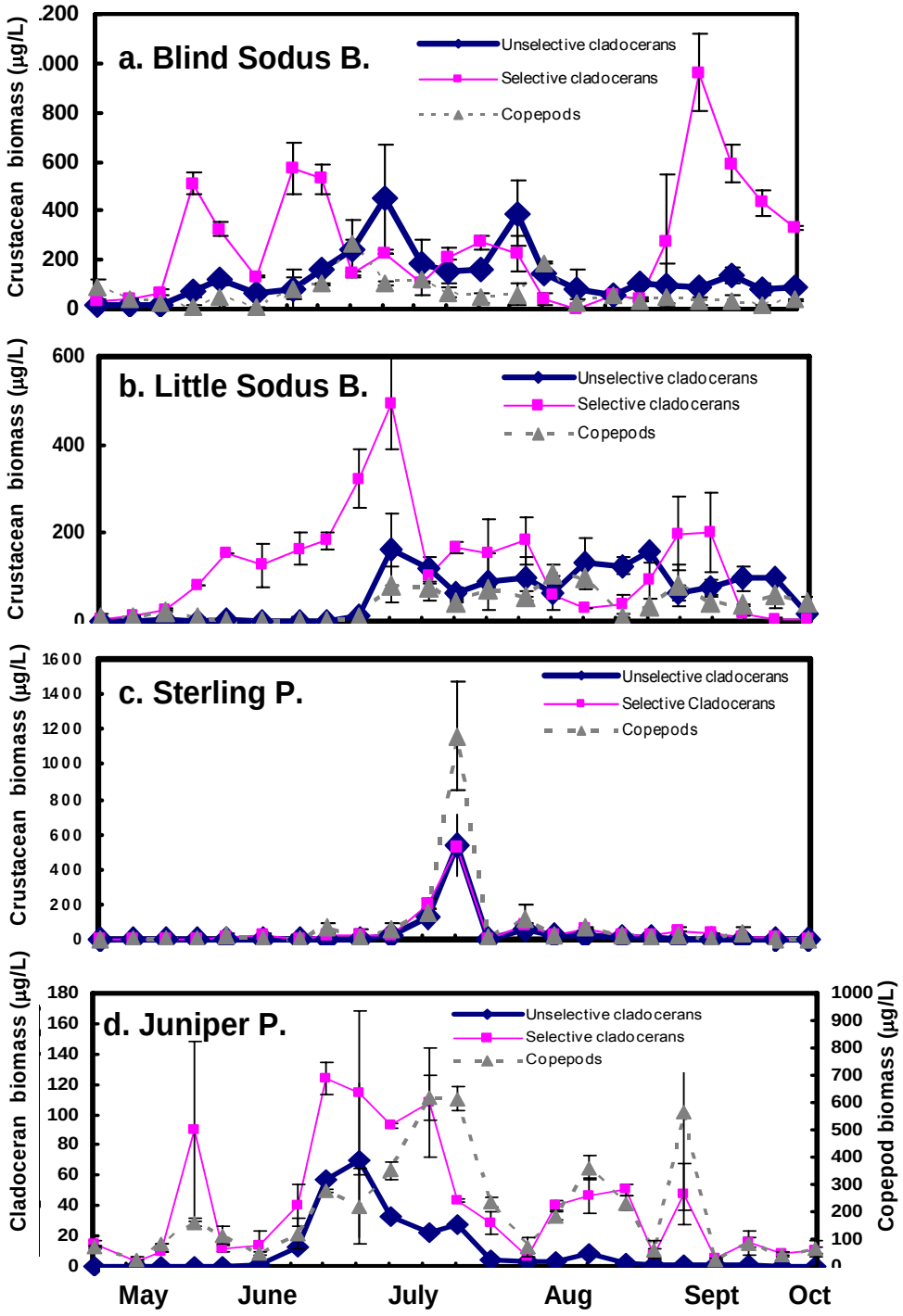
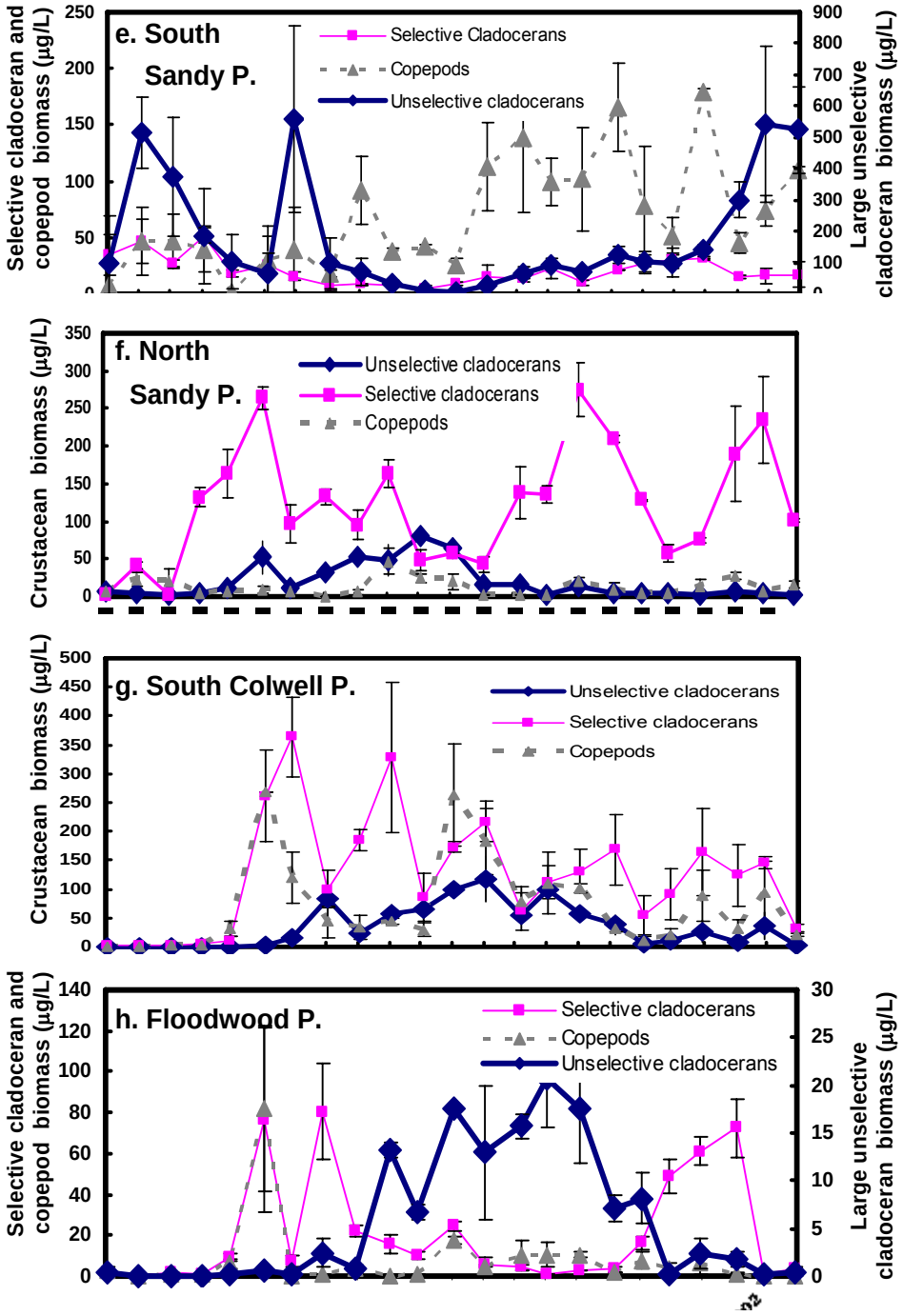

a. Blind Sodus B.
Unselective cladocerans
Selective cladocerans
Copepods
Crustacean biomass (µg/L)
b. Little Sodus B.
c. Sterling P.
Selective Cladocerans
d. Juniper P.
Cladoceran biomass (µg/L)
Copepod biomass (µg/L)
May
June
July
Aug
Sept
Oct

Figure A.2 continued



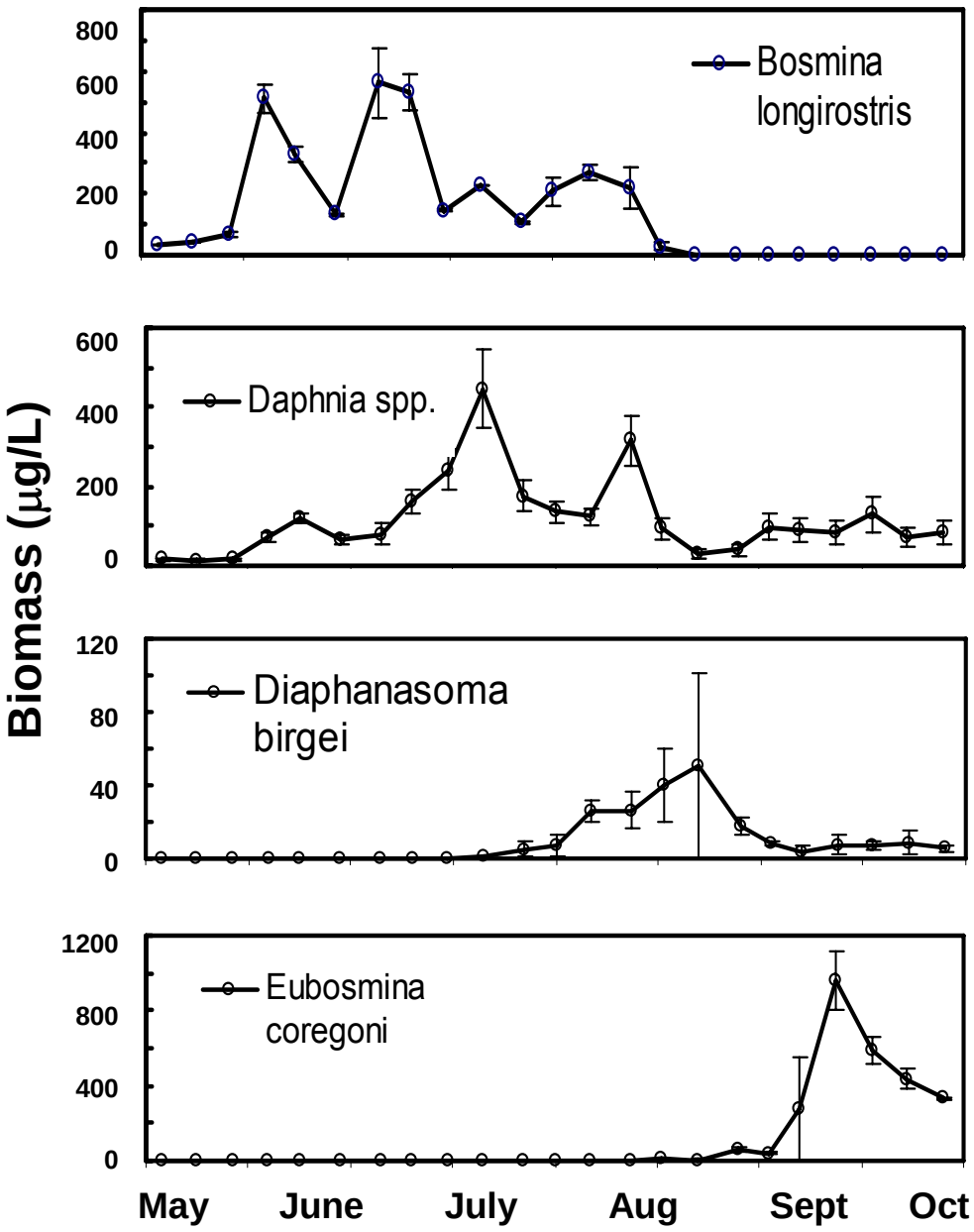


Figure A.3 Cladoceran succession in 2002 Blind Sodus B. zooplankton community. Error bars represent +/- 1 s.e.

zooplankton biomass was in the lower half of the embayments, it held the second most diverse zooplankton community.

Community dynamics: The growing season in Little Sodus B. started with a large spring phytoplankton bloom comprised almost entirely of centric diatoms (Fig. A.1b). The biomass of edible taxa fluctuated, but remained at intermediate levels throughout the period of study, unlike the inedible phytoplankton which peaked in late summer. A distinct decrease in biovolume of edible phytoplankton occurred in early July, as did that of inedible taxa. Both groups rebounded, and then edible phytoplankton gradually decreased though late August and early September as inedible phytoplankton began to dominate, due in large part to a late-summer bloom in typical large spring species, including *Fragilaria, Asterionella*, *Dinobryon, Ceratium,* and *Aulacoseira* (Fig. A.4a). At the same time that these spring species increase again, the large *Anabaena* population crashed, before rebounding one week later, but with no heterocysts (Fig. A.4b). Both inedible and edible groups reached peak biovolume in mid-September, the edible group bolstered by a large population of large cryptomonads and *Fragilaria* (Fig. A.1b). The phytoplankton population then declined to a low biovolume value by the end of the season.

The zooplankton community in Little Sodus B. started out growing slowly from a low total biomass comprised primarily of cyclopoid copepods during a relatively low density spring algal bloom (Fig. 1.4b). Populations of rotifers and small cladocerans began to increase in early June and then declined as both copepods and large cladocerans reached high biomass in early July (at the same time that edible biovolume decreased (Fig. 1.2b). Total crustacean biomass fluctuated throughout July and August, and rotifers did not rebound until the end of the growing season. In

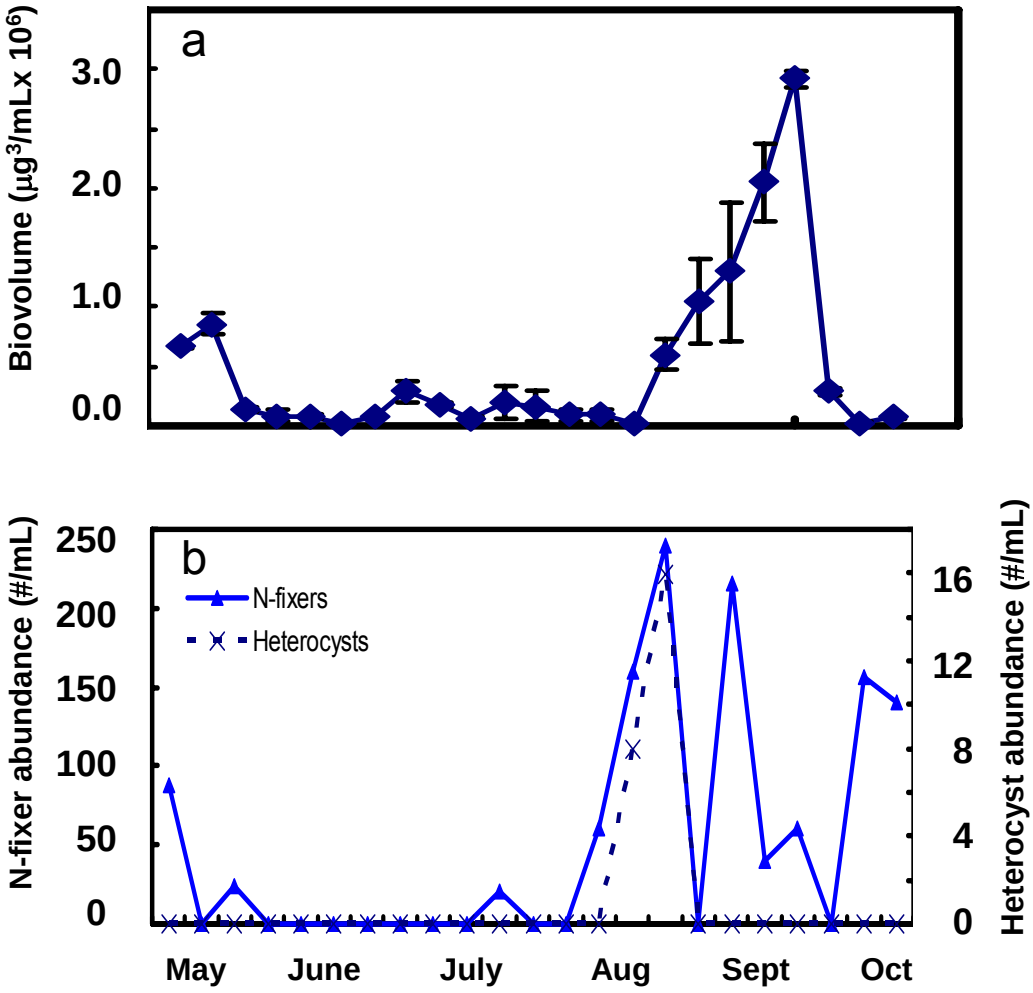


Figure A.4 2002 Little Sodus B. phytoplankton dynamics; cold-water species (diatoms, *Dinobryon* sp., *Ceratium* sp.) biovolume (a) and N-fixer, heterocyst abundance (b). Error bars represent +/- 1 s.e.

general, high-r species dominated the Little Sodus B. biomass through the first half of the growing season, but were then replaced by low-r large cladocerans and copepods.

Sterling Pond

Seasonal averages: Sterling P. supported the second highest total seasonal mean phytoplankton biovolume of the eight embayments, as well as the highest edible phytoplankton biovolume, taxon richness, and diversity (Table A.1). This large biovolume was driven by high relative chrysophyte abundance, as well as moderately high levels of all the other taxonomic groups. Cyclopoid copepods dominated the zooplankton (31% of mean seasonal biomass), with all life history stages in high abundance relative to the other embayments.

Community dynamics: Phytoplankton was abundant in Sterling P. in June and July, but otherwise low in total biovolume (Fig. 1.4c). There was a peak of edible species in early June comprised of small quadrate diatoms, *Fragilaria*, microflagellates, and a few edible chlorophyte species (i.e., *Chlamydomonas* and *Ankistrodesmus*) (Fig. A.1c). Larger, less edible diatoms came to dominance in the following weeks before many of the populations that had been found in the June 3 phytoplankton community bloomed again in early July, joined by a large population of *Chlorella*. There was a second phytoplankton peak later in July composed of less edible cyanobacteria, dominated by heterocyst-bearing *Anabaena* and *Oscillatoria*, as well as large populations of *Aulacoseira* and large-celled *Fragilaria*. Phytoplankton became scarce after the end of July and remained at low density throughout the remainder of the growing season.

The Sterling P. zooplankton was low in density during all of the growing season except for a single date in mid-July (Fig. 1.4c). This brief peak (captured in

both replicate samples on that date) was comprised of rotifers, large and small cladocerans, and cyclopoid copepods (Fig. A.2c). This zooplankton peak coincided with the peak in inedible phytoplankton described above (Fig. A.1c). This peak also coincided with the first date on which significant amounts of benthic cladocerans were captured in the water column, including *Sida crystallina* and *Simocephalus* sp. These species continued to be present in plankton samples through late September and their presence generally corresponds with periods of high macrophyte abundance at the sampling site.

Juniper Pond

Seasonal averages: Juniper P. contained the highest seasonal mean phytoplankton biovolume of any of the embayments, with the highest inedible and second lowest edible biovolume (making it 68% inedible, Table A.1). Juniper P. also had much higher phytoplankton species richness than the other embayments, with eleven more taxa than the next highest embayment, Sterling P. Despite the high level of phytoplankton inedibility, there was only a very small population of cyanobacteria in Juniper P., with N-fixers comprising only 0.05% of the total biovolume. Instead, the high inedibility numbers were driven by large cell and colony sizes. The zooplankton community was dominated by copepods, which comprised 65% of the total biomass, which was intermediate in comparison with the other embayments. It had greater than four times the calanoid copepod biomass of any other embayment, and more than twice the density of total copepods. Rotifers and cladocerans were at low relative abundances, and the copepod dominance resulted in low crustacean species richness and diversity.

Community dynamics: Low Juniper P. spring phytoplankton biovolume (Fig. A.1d) was comprised of predominantly inedible taxa in late May and early June, during which the plankton biovolume consisted mainly of large colonial chrysophytes and diatoms, including *Dinobryon*, *Tabellaria,* and *Fragilaria*, and the dinoflagellate, *Glenodinium*. These species were replaced in June by cyanobacterial species, dominated primarily by heterocyst-bearing *Anabaena* spp. as well as *Microcystis* and *Oscillatoria*. These inedible species dominated the system at low numbers through July until they were replaced primarily by another group of large chrysophytes, dinoflagellates, and euglenoids. The first peak of edible taxa occurred in September, when a highly edible and diverse group of cryptophytes, diatoms, and chlorophytes including *Chlamydomonas, Oocystis,* and *Selenastrum* dominated. This edible assemblage declined markedly in October, when the water column was again filled with large, silica-dependent species like *Tabellaria*.

The zooplankton community in Juniper P. showed a spring peak in total biomass that followed the phytoplankton peak by one week (Fig. 1.4d). The spring population was comprised predominantly of rotifers, cyclopoid copepods, and small cladocerans, and was followed temporally by a large peak in zooplankton biomass in late June when these smaller grazers were replaced first by large cladoceran grazers such as *Diaphanosoma* and *Ceriodaphnia*, as well as growing populations of both cyclopoid and calanoid copepods (the dominant crustacean grazers in Juniper P.) during the last half of July (Fig. A.2d). By September, the large grazers were almost entirely replaced by the small cladoceran (*Bosmina, Chydorus)* and rotifer populations seen earlier in the season, while calanoid copepods continued to dominate the system before virtually everything crashed out, with zero positive growth for any of the groups during the last few weeks of the growing season. While copepods dominated the system numerically, the large unselective cladocerans appear to have exerted the

most influence on the edible phytoplankton community, which did not bloom in large numbers until the unselective cladoceran population had crashed out of the system (Fig. A.5).

South Sandy Pond

Seasonal averages: South Sandy P. supported the most diverse phytoplankton assemblage of the eight embayments with an intermediate biovolume (Table A.1). Numerically, it had the highest phytoplankton abundance for all taxonomic groups, and one of the highest total biovolumes across all groups as well, with the exception of the chrysophytes. The phytoplankton community was the lowest among the embayments in terms of percent edibility (31%), in part because it also contained the highest percentage (by biovolume) of N-fixing cyanobacteria at 39%. The zooplankton community was the third greatest in terms of total biomass, and included both the largest percentage of unselective cladocerans (comprising on average over the season 69% of the total biomass) and predatory invertebrates. It also contained the second highest mean biomass of both calanoid copepods and *Daphnia.* The biomass of small selective cladocerans was very low relative to the other systems. The dominance by a few large unselective grazers resulted in the lowest crustacean diversity measured.

Community dynamics: South Sandy P. phytoplankton biovolume peaked on three dates during 2002: late May, late-June, and late August (Fig. 1.4e). Chrysophytes and diatoms contributed to these peaks and were abundant throughout the year, particularly *Uroglenopsis* and *Aulacoseira*, which dominated the final half of the major August bloom. Edible taxa dominated the mid-summer biovolume (Fig. A.1e). Cyanobacterial species were also present through the year and added to all three

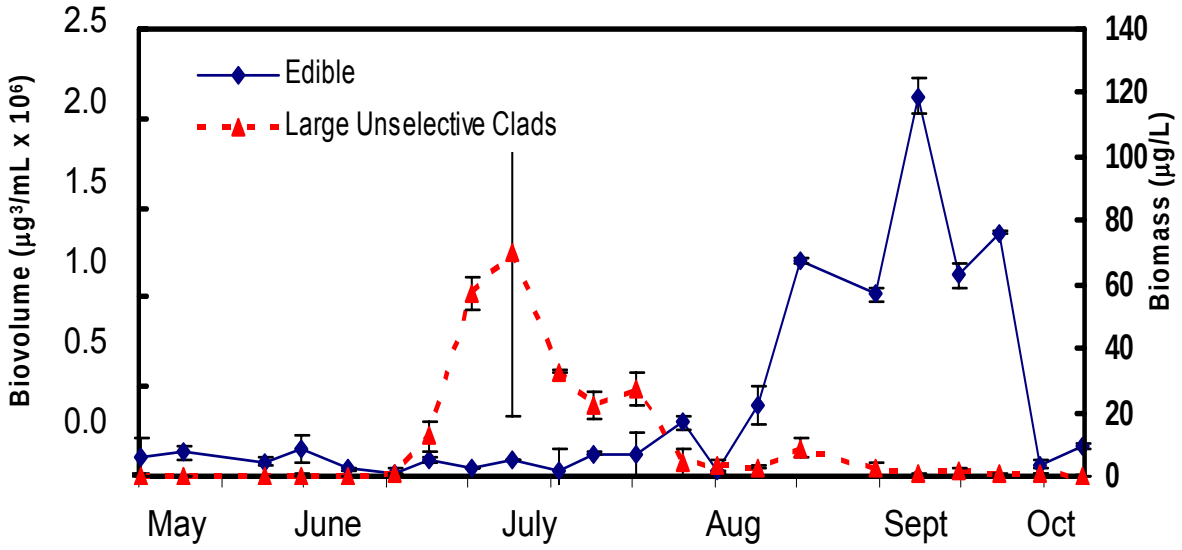


Figure A.5 2002 Juniper P. edible phytoplankton and large unselective cladoceran community dynamics. Error bars represent +/- 1 s.e.

biovolume peaks, particularly the N-fixing species *Aphanizomenon*, which was present on all but two of the sampling dates. Heterocyst-bearing *Anabaena* species were also present throughout the season, starting in late May, and dominated the second and the beginning of the third phytoplankton peaks. The final fall phytoplankton community was dominated by a suite of cyanobacterial species, in particular *Microcystis* and *Aphanizomenon*.

South Sandy P. zooplankton was also dominated by a limited number of species, especially unselective cladocerans and copepods (Fig. A.2e). Two peaks in zooplankton density early in the season, dominated by *Daphnia* and *Eubosmina*, immediately preceded the two early season phytoplankton blooms (Fig. A.6e). *Daphnia mendotae* was present predominantly early in the season, and *Daphnia retrocurva* became increasingly abundant as the season progressed (Fig. A.2e). *Diaphanosoma* added significantly to the large cladoceran biomass as well later in the season when *Daphnia* populations waned. Both cyclopoid and calanoid copepods contributed to the late season zooplankton biomass as well, along with rotifers and small cladocerans, which were present during the first and last zooplankton peaks (with *Eubosmina* dominating the first peak and *Bosmina* dominating the second, Fig. A.6). A small *Leptodora kindtii* population was present throughout the season.

North Sandy Pond

Seasonal averages: North Sandy P. had intermediate phytoplankton and zooplankton densities relative to the other systems (Table A.1). The phytoplankton community contained both small edible and large inedible groups, including the second largest density of cyanobacteria resulting in a low mean edibility of 40% over the course of the growing season. Zooplankton had the highest numerical abundance of any embayment, but because small rotifers were prevalent, this did not translate into high

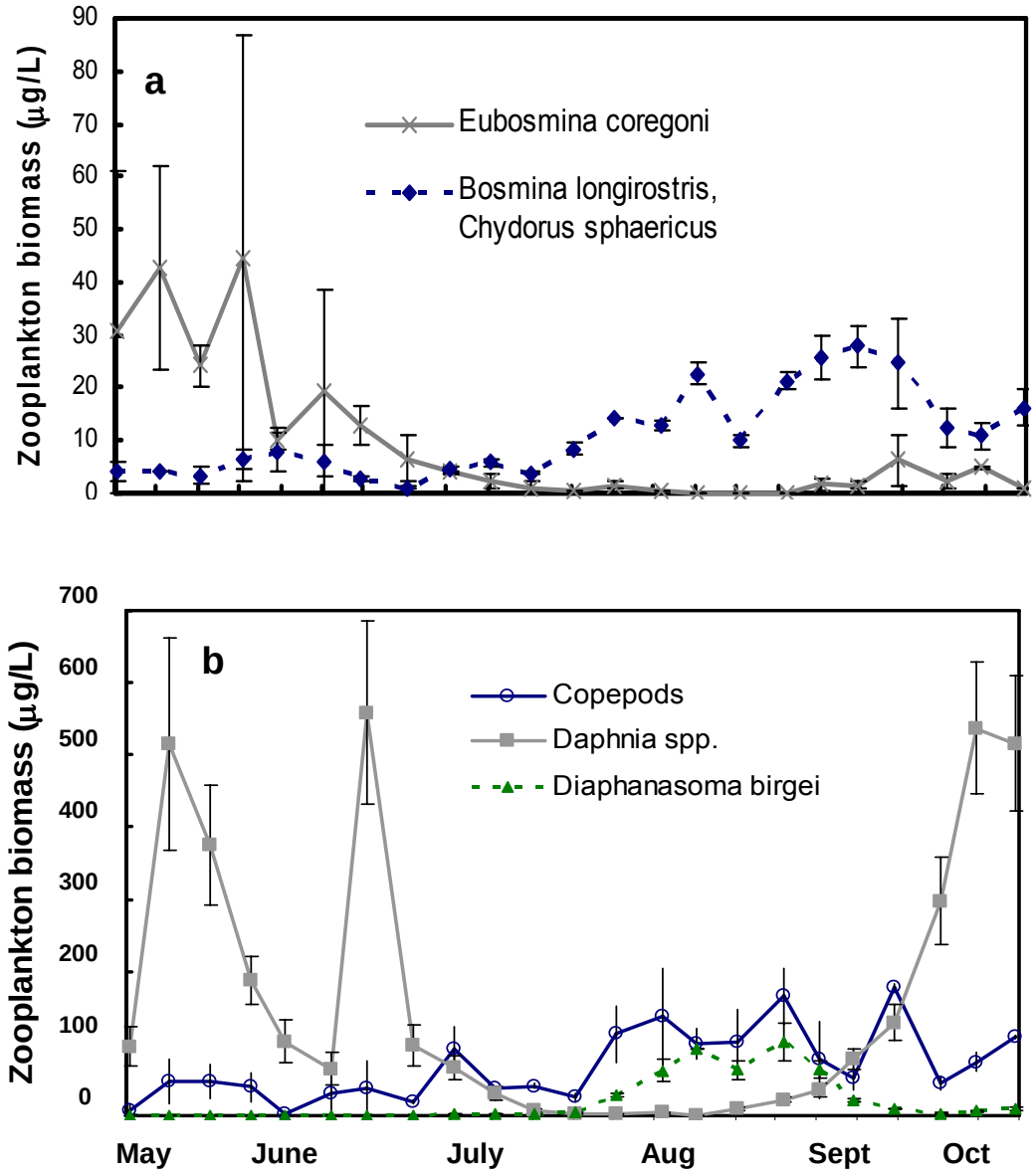


Figure A.6 2002 South Sandy P. high (a) and low (b) r_{max} zooplankton dynamics. Error bars represent +/- 1 s.e.

biomass, which was the second lowest of the embayments. All other zooplankton groups were only moderately abundant, with cyclopoid copepods and small selective cladocerans comprising much of the overall biomass. Whereas the phytoplankton community was only moderately diverse, the zooplankton community ranked as both the most rich and diverse of the eight embayments.

Community dynamics: The phytoplankton population in North Sandy P. in May, was comprised predominantly of cryptomonads, *Dinobryon,* and *Asterionella* (Fig. 1.4f). This modest bloom represented the largest abundance of edible phytoplankton throughout the growing season (Fig. A.1f), and was followed immediately in mid-June by the first of three peaks of inedible taxa. The latter two peaks occurred in August and at the end of the growing season in October. While the first and second inedible peaks were dominated by large diatoms like *Fragilaria, Asterionella,* and *Aulacoseira*, cyanobacteria strongly contributed to the end of season bloom when heterocyst-containing *Anabaena* appeared.

For zooplankton biomass, (Fig. 1.4f), a peak in early June was comprised of rotifers and large cladocerans. *Daphnia retrocurva* and *D. mendotae* dominated in mid-July along with cyclopoid copepods, while smaller zooplankton decreased in abundance before rebounding following a decline in large cladocerans at the end of July (Fig. A.2f).

South Colwell Pond

Seasonal averages: South Colwell P. had the third lowest mean seasonal phytoplankton biovolume of the eight systems, but the highest numerical abundance of edible phytoplankton taxa resulting from the presence of many small cells in the early spring bloom (Table A.1, numerical abundance not listed). The pond, however, also

had the second highest percentage of N-fixing species by biovolume, but the lowest ratio of heterocysts to vegetative cells. The zooplankton community had the second highest mean seasonal biomass, with relatively high densities of all functional groups. Diversity of both phytoplankton and zooplankton was intermediate, even though South Colwell P. had low phytoplankton species richness.

Community dynamics: South Colwell P. phytoplankton biovolume was dominated by inedible taxa throughout most of the season, with edible species contributing to over half of the biovolume only during the early spring bloom (Fig. A.1g). This early spring assemblage was predominantly comprised of cryptomonads, pennate diatoms, and large colonies of *Fragilaria* and *Dinobryon*. Three peaks of inedible phytoplankton were spaced throughout the season, and all three were dominated by N-fixing cyanobacteria species, particularly *Anabaena*. Heterocysts were abundant only in June and July.

Zooplankton biomass was very low throughout May, increased in mid-June and then fluctuated throughout the remainder of the season (Fig. 1.4g). Rotifers were the first group to appear in spring, followed by copepods and small cladocerans in mid-June (Fig. A.2g). These populations decreased as large unselective cladocerans increased in the following weeks. Each of these functional groups fluctuated around moderate levels throughout the rest of the season. The biomass of edible phytoplankton taxa decreased as crustacean biomass increased in early June, and then remained essentially constant at an intermediate density throughout the rest of the season as crustaceans remained in the water column.

Floodwood Pond

Seasonal averages: Mean seasonal total phytoplankton biovolume was low (higher only than Little Sodus B.), with cyanobacterial densities particularly low relative to all other systems (and comprising only 0.1% of the total biovolume, Table A.1). The community was dominated instead by edible species (69% of total biomass). Zooplankton biomass was low, only a quarter of that of the next largest zooplankton embayment community. Rotifer abundance was intermediate, but each of the other functional groups was lowest in biomass. Copepods and small selective cladocerans comprised much of the mean seasonal zooplankton biomass. Although both phytoplankton and zooplankton taxon richness was relatively high in Floodwood P., diversity was relatively low.

Community dynamics: The season began in Floodwood P. with a bloom of inedible phytoplankton, made up of large colonial chrysophytes like *Dinobryon*, which was abundant throughout the season (Fig. A.1h). Chrysophytes and large diatoms dominated the inedible phytoplankton functional group throughout the season, while cyanobacteria never reached high numbers. Both edible and inedible phytoplankton bloomed in early July before a large increase in inedible taxa in mid-July. There was one final bloom of large chrysophytes and diatoms in mid-August before the largest peak of edible phytoplankton, comprised predominantly of cryptomonads, in late August. The phytoplankton community gradually declined to negligible abundance throughout the remainder of the season.

Zooplankton biomass was relatively low compared with the other embayments throughout the growing season (Fig. 1.4h). Density was very low until late May, when rotifers increased, followed soon after by a short-lived peak of copepods and small cladocerans (Fig. A.2h). Large unselective cladocerans did not appear in

notable biomass until July and were present through September at low numbers. Their density was at its maximum throughout July and August when other zooplankton groups were at their minimum. Large cladocerans declined in September as small cladocerans, rotifers, and copepod nauplii rose before declining precipitously in early October.

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CHAPTER 2

OF WIND AND WATER: INSIGHT INTO THE REGULATORY ROLE OF UPWELLINGS IN FRESHWATER EMBAYMENT PROCESSES

Introduction

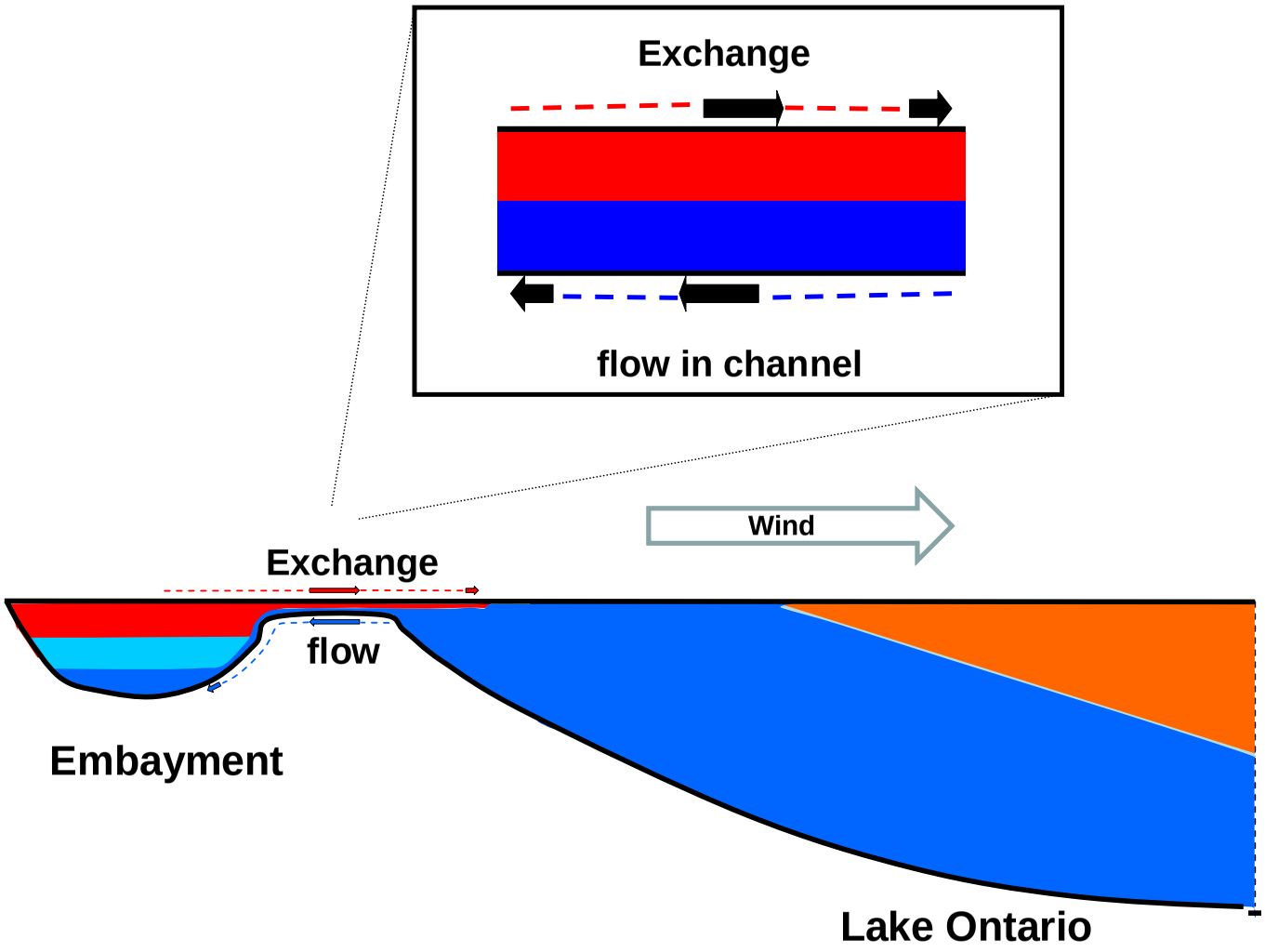
Lake ecosystems can be thought of as both self-contained "microcosms", with boundaries clearly delineated by their shorelines (Forbes 1887; Hutchinson 1964; Hairston 2005), and as habitat patches strongly connected to their surrounding terrestrial landscapes via tributary flow, overland run-off, and atmospheric deposition (Likens 1974; Hanson et al. 2003; Carpenter et al. 2005). The relative importance of ecological interactions internal to the lake basin in comparison with the effects of external forcing and subsidies depends critically upon such things as basin size, strength and temporal variability of connectivity to the external environment, and the strengths of biogeochemical and interspecific interactions within the lake relative to the magnitudes and kinds of external inputs. These links beyond the shoreline are particularly apparent in freshwater embayment systems, basins directly connected to an adjacent larger body of water but separated by coastal sediment deposition across the mouth of a tributary. The connection can range from permanent (often artificially maintained) channels connecting the embayment to its adjacent lake, to transient openings, to subsurface flow through a gravel bar or sandbar. Thus, these embayment systems are not only influenced by terrestrial inputs from the watershed, but can also be impacted directly by bidirectional exchange flow with the larger body of water.

This additional external connectivity creates an unusual challenge for the resident taxa that make up the embayment plankton because they are exposed to an influx of organisms from the adjacent lake that are much more similar in habitat

requirements than are those that might be transported in from upstream in the watershed. In addition, fish can actively swim in and out of an embayment, often using it as a spawning ground, bringing nutrient subsidies and increased predation pressure with them (Boehlert and Mundy 1988, Klumb et al. 2003, Meixler et al. 2005, Moore et al. 2007, West et al. 2010). As a result, plankton communities in embayments are exposed, and potentially vulnerable, to external forcing in the form of both biotic introductions and chemical (nutrient) and physical forces originating outside of the system.

One of the external forces influencing embayment plankton communities is an upwelling event in the large lake that causes exchange flow between the two water bodies as cold up-welled water in the large lake flows by gravity into the embayment, in turn forcing warm surface water out into the lake (Fig. 2.1). Upwelling and exchange flow occur in summer when both the large lake and the embayment are thermally stratified. Warm surface waters in the large lake are driven offshore by persistent winds and are displaced by cold hypolimnetic water pushed up into the near-shore euphotic zone. Upwelling events have been intensively studied in coastal ocean environments as well as in large lakes, with a particular focus on the influx of nutrients that the cold water brings to the surface (Schelske et al. 1971, Richards 1981, Rosenfeld et al. 1994, Hill et al. 1998, Pitcher et al. 2010). The effect of upwelling on water exchange with embayments along the shoreline has received much less attention. Marine research has demonstrated the impact of saline intrusions into coastal bay ecosystems, much of which has focused on the large effects of the saline mixing (Fram 2007, Ryan 2009, Eichler 2010). Similar exchange flow between two freshwater systems is distinct because the salinities of the two water bodies are similar, and so are driven purely by temperature-related density differences rather than salinity (or salinity and temperature) in marine cases. A potentially significant

Figure 2.1 Diagram of upwelled water exchange between large lake and coastal freshwater embayment. In this situation, cold hypolimnetic water is upwelling along the shoreline of the large body of water. This water is dense compared to the warm epilimnetic water of the adjacent shallow embayment system, and thus flows along the bottom of the connecting channel, following the basin bathymetry into the embayment. This cold, dense water fills the embayment from the bottom-up, displacing the warmer embayment water out into the surface of the lake.


Exchange
flow in channel
Wind
Exchange
flow
Embayment
Lake Ontario

difference between inland water and marine upwelling events is, then, a much greater likelihood of successful biological exchange between a large lake and a connected embayment, because of the absence of an osmotic barrier.

Upwelling-driven exchange flows may also bring water with a distinct nutrient signature into an embayment accompanied by a direct response of the resident plankton community. In marine and lake coastal environments, upwelling events are well known for inducing high productivity when they introduce nutrients into a nutrient-deprived near-shore euphotic zone. However, upwelling-driven exchange with adjacent embayments is distinct from simple coastal upwelling, both because it involves water movement between two separate bodies of water, and because the relative productivities of the primary water body and the embayment may differ markedly. Unlike non-embayment coastal upwelling where cold nutrient-rich water rises into a nutrient-deprived photic zone, embayments, because of their intimate connection to the watershed, are typically nutrient-enriched relative to the adjacent large lake. Upwelling-driven exchange flow has the potential to fill an embayment with relatively nutrient-poor water, negating any possibility for the increased biological productivity generally associated with upwelling events and potentially leading to decreased productivity. Rueda and Cowen (2005) suggested that upwelling-driven flow could be the most important exchange of water masses between these adjacent freshwater systems, yet there are only a few examples of studies documenting exchange flow transport between large inland water bodies like the Laurentian Great Lakes and their coastal embayments (Dunstall et al.1990, Churchill et al. 2004, Wells and Sealock 2009).

As a part of a more comprehensive multi-investigator study of eight embayments and the effect of their level of connectivity to Lake Ontario on plankton dynamics, Rueda and Cowen (2005) analyzed the hydrodynamic properties of

exchange flow with a large, well connected embayment, Little Sodus Bay, on the Lake Ontario's southern shore, and found the introduction of upwelled water to the embayment to be extensive. This raises the question of how important such exchange flows can be to the transfer of planktonic organisms from the large lake to the embayment. We explore this question for two significant (hurricane induced) weather-driven upwelling events, in two years, for two embayments along the southern shore of Lake Ontario.

The importance of exchange flows for plankton movement depends upon how frequently they occur and on how long each event lasts. An analysis of 26 years of data for water temperatures along the southern shore of Lake Ontario shows (as described below in greater detail) that an average of nearly five events occurs per year, between two and three of which last at least four days. This suggests that such events have the potential to be important both in introducing species from one water body to the other and as an influence on embayment plankton dynamics.

Our study was designed to explore the several specific upwelling events in two embayments. First, we compare the theoretical and simulation results of Rueda and Cowen (2005), which projected the exchange flow behavior between the two systems during events in 2002, with data we had collected as part of a routine sampling effort in that year. These include weekly samples for physical, chemical, and biological variables at Little Sodus Bay, but because each of the two upwelling events in that year lasted only about a week, subsequent retrospective analysis of our weekly sampling data revealed only a hint that these physical forcing events could be significant drivers of the dynamics of the resident plankton populations (Doyle-Morin, Chapter 1). As a result, in 2003 and 2004 we carried out focused field studies of the pelagic portions of two embayment-large-lake systems at short sampling intervals

during upwelling events. Our field study compared the effects of Lake Ontario upwelling on the coastal dynamics of Little Sodus Bay and another neighboring embayment system, Sterling Pond. These two water bodies have similar connectivity with the lake, but differ in total surface area, bathymetry, and the sizes of their respective watersheds. A comparison of these two embayments permits an exploration of the effect of external physical forcing, impinging upon embayment-specific chemical and biological characteristics, on the internal dynamics of the planktonic communities. Our objective was to look, during conditions of upwelling, for physical and chemical signatures of exchange flow (e.g., summer-time appearance of cold, dissolved oxygen-rich water in the embayment hypolimnion), and evidence of the appearance Lake Ontario plankton taxa in the embayments where they are otherwise absent.

Methods

Study site description

The two embayments of this research are located along the southern shoreline of Lake Ontario, both within the confines of Fairhaven State Park in Fairhaven, NY (Fig. 2.2). Little Sodus Bay (LSB) (43°20'00"N, 76°42'30"W**)** is the larger of the two systems (4.69 km^2 surface area, 4.31 m median depth, 12.0 m maximum depth). It has a very small watershed (6.84 km^2), only slightly larger than the embayment itself, and is predominantly connected to the surrounding landscape by direct run-off, although there is a single small tributary with a mean daily discharge of 0.154 $m^3 s^{-1}$. LSB is permanently connected to Lake Ontario through a large (550 m long, 75 m wide) and shallow (2-3 m deep) artificial channel maintained for boating traffic. Due to its depth, LSB is predominantly an open-water pelagic habitat, and supports a planktonic community typical of a large lake (Doyle-Morin, Chapter 1).

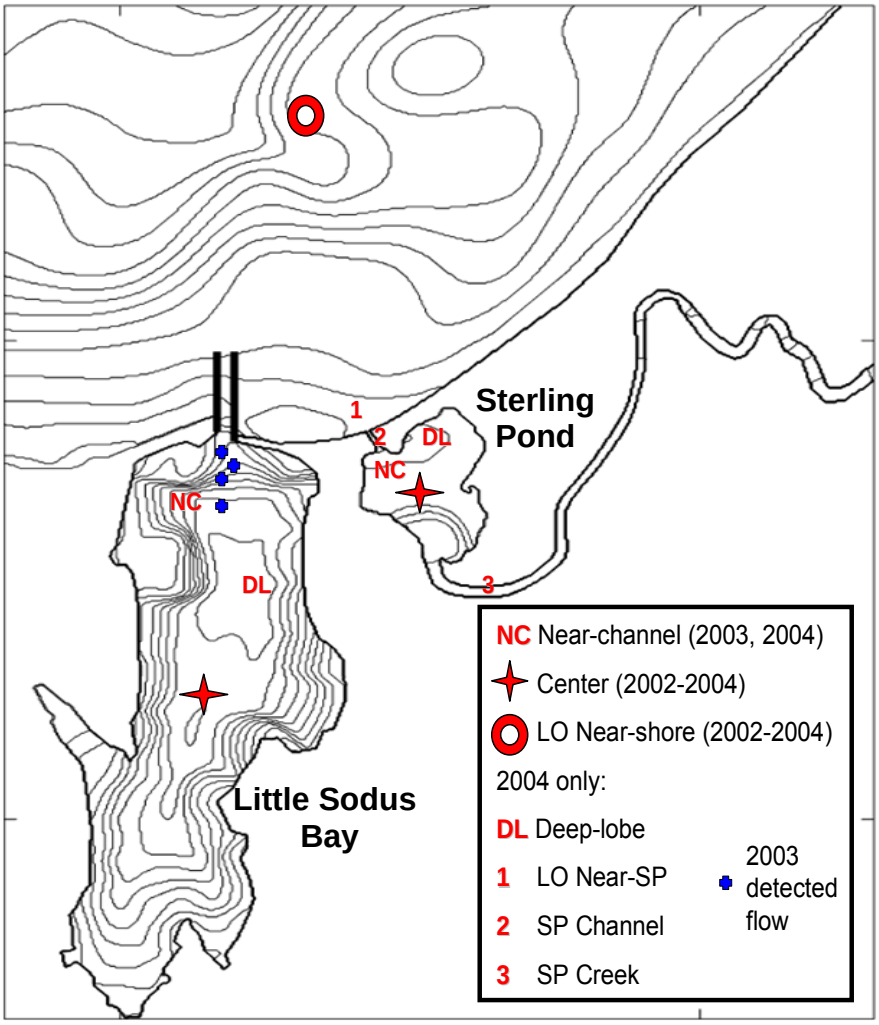


Figure 2.2 Map of LSB and SP, with sampling locations denoted. Bathymetric contours are depicted at 1 m intervals. Figure provided by A.King.

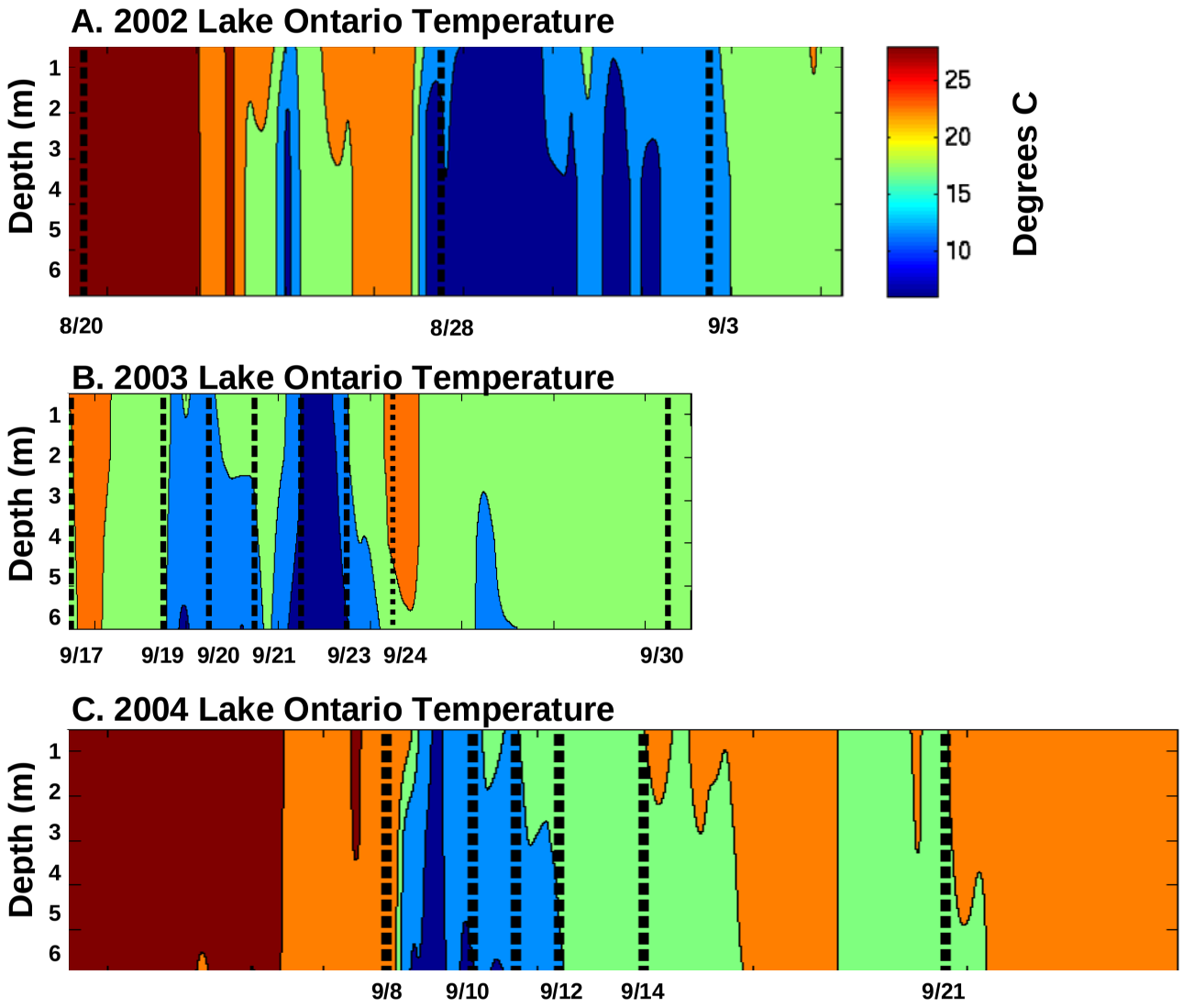
Sterling Pond (SP) (43°20'30"N, 76°42'00"W), 1 km east of (LSB), is smaller than LSB (1.01 km^2 surface area, 0.98 m median depth, 5.0 m maximum depth) but with a much larger watershed (202.3 km^2), nearly 200 times the embayment's surface area. This embayment is fed by a large tributary, Sterling Creek, which is 149.83 km in length with a mean daily discharge of 3.63 $m^3 s^{-1}$. SP is also permanently connected to Lake Ontario by an artificial channel (17 m wide, 2.5 m maximum depth, 140 m long). The shallow bathymetry of this embayment supports a predominantly littoral community dominated by dense macrophyte growth. There is an area of open-water habitat year-round in the deepest eastern lobe portion of the embayment (hereafter "deep lobe").

To compare environmental variables of the embayments with those of near-shore Lake Ontario (LO), we established a study site 2 km offshore (43°22'30"N, 76°42'15"W), directly north of the channel openings for the two embayments (Fig. 2.2). The maximum pre- and post-event water depths at this site (during calm conditions) ranged from 12-13 meters.

Event description

We analyzed the effects of three upwelling events of varying duration and apparent effect. The exchange flows during these events were the result of a combination of baroclinic, or temperature- and density-driven forces, and barotropic, or water-elevation and pressure-driven, forces. The first event, 28 August - 4 September 2002, was a sustained baroclinic event that brought upwelled hypolimnetic LO water along the southern shoreline for over a week. Although this event did not include associated precipitation, there was an additional small wind-driven exchange event preceding the sustained event (Fig. 2.3a). The second upwelling event, 19 - 23 September 2003, also did not include associated precipitation, but was a shorter-

Figure 2.3 Interpolated 2002 (a), 2003 (b), and 2004 (c) time-depth temperature profiles in LO near-shore water column. Thermister strings set at one meter intervals recorded data continuously (1 hour increments) from surface to bottom. Dashed lines represent routine weekly (a) or event-based sampling dates (b,c). (E.A. Cowen and A.T. King, personal communication)


A. 2002 Lake Ontario Temperature
Depth (m)
1
2
3
4
5
6
8/20
8/28
9/3
25
20
15
10
Degrees C
B. 2003 Lake Ontario Temperature
Depth (m)
9/17
9/19
9/20
9/21
9/23
9/24
9/30
C. 2004 Lake Ontario Temperature
Depth (m)
9/8
9/10
9/12
9/14
9/21

duration, baroclinic and barotropic pulsing event in which upwelling LO water was displaced along the shoreline for two relatively brief (1 – 2 day) intervals (Fig. 2.3b). The third event, 10 -14 September 2004, was a short-duration (3-4 days) sustained event that included precipitation and thus barotropic forcing from the watershed in addition to the baroclinic forcing from Lake Ontario (Fig. 2.3c).

Retrospective data analysis – long-term frequency of exchange flow

Rueda's and Cowen's (2005) analysis of exchange flow between Lake Ontario and Little Sodus Bay, suggested that when upwelling water is sufficiently cold and dense (ca. 5 °C cooler than the embayment surface water), and if the upwelling event is sufficiently long (≥ ca. 4 d.), extensive exchange is possible. Surface temperatures in Little Sodus Bay typically exceed 20 °C, so once near-shore Lake Ontario temperature is depressed to 15 °C exchange flow is expected. We used near-shore Lake Ontario, surface temperature data collected near Fairhaven State Park, Fairhaven, NY, for the 26 years between 1976 and 2001 to determine the frequency of occurrence of upwelling conditions along the shoreline (Jim Nugent, personal communication). We identified the periods during summer thermal stratification in Lake Ontario that water temperature was ≤ 15 °C, and then aggregated these data into categories of shorter-duration events (≤ 3 consecutive days of cold water), longer-duration events (≥ 4 consecutive days) and pulsing upwellings that fluctuated between warm and cold near-shore water with a frequency less than two days.

Retrospective data analysis – 2002 upwelling event

We analyzed our routine weekly sampling data for the longer-term, sustained upwelling event in 2002. Rueda and Cowen (2005) documented upwelling-driven

exchange flow between LO and LSB using hourly temperature data from a set of vertical thermistor strings deployed in near-shore LO and in LSB. They used these data to model the water exchange dynamics during the event. We compared their results to the limnological data we collected weekly at a central site in LSB and bi-weekly in LO, from May - October 2002. Temperature and dissolved oxygen profiles (Yellow Springs Instruments Model 58) were recorded at half-meter to one-meter intervals throughout the water column. Phytoplankton samples were collected using a tube sampler that integrated the entire water column, and preserved in 1% Lugol's solution. Cells were identified to genus or species, measured with an eyepiece micrometer, and counted using a Wild M40 inverted microscope. Phytoplankton densities were expressed as individuals mL^{-1} or converted to biovolume (μm^3 mL^{-1}) based on cell dimensions (Wetzel and Likens 2000). Zooplankton were collected by diagonal tow using a Clarke Bumpus quantitative sampler fitted with a 75-µm-mesh net and preserved using 70% ethanol. Individuals were identified to species, measured with an eyepiece micrometer, and counted using an Olympus SZH10 dissecting microscope. Biomasses were calculated using length-weight regressions from Bottrell et al. (1976). Plankton were categorized into functional groups (i.e., edible and inedible phytoplankton) based on size and taxon as described in Doyle-Morin et al. (Chapter 1). Because we did not anticipate this event and only have data collected at predetermined weekly intervals, we treat this analysis as "retrospective". Physical dynamics are outlined below, while the biological response is discussed in greater detail elsewhere (Doyle-Morin, Chapter 1).

Upwelling event sampling

In 2003 and 2004 we were able to anticipate upwelling events associated with the remnants of hurricanes that passed inland over Lake Ontario late in the summers of

those years. We carried out intensive sampling before, during, and after upwellings and exchange flows with LSB and SP. Sampling consisted of temperature and dissolved oxygen profiles at 0.5 – 1.0 meter intervals throughout the water column, plus water samples for phytoplankton and zooplankton at depths half-way through the epilimnion and half-way through the hypolimnion, using the pre-upwelling thermocline to determine these depths. SP was too shallow to stratify, so samples were collected from a single mid-depth location at each site. Sampling was completed in both 2003 and 2004 at a central and near-channel site in both embayments in order to track the influence of the event as it moved further into the embayment. In 2004, an additional "Deep-Lobe" site was added at the deepest location in each embayment (Fig. 2.2) to sample the point of deepest bathymetry where the cold intruding water from LO would first begin to pool during an upwelling event (Fig. 2.2). We also collected physical data immediately outside of the SP channel in LO (hereafter "LO Near-SP") and upstream in SP Creek (Fig. 2.2) during this event.

For the 2002 and 2003 upwelling events, an Acoustic Doppler Current Profiler (ADCP) was deployed in the SP channel to measure water-flow direction and temperature as a function of water depth during exchange flow between the embayment and Lake Ontario. Government navigation restrictions did not permit equipment to be deployed in the LSB channel, although temperature and dissolved oxygen data collected daily at 0.5 m increments from surface to bottom confirmed similar flows for each event in the LSB channel. Dissolved oxygen and temperature data were similarly collected in both channels in 2004. Note that because we were not allowed to collect ADCP data in the LSB channel, we assume that the SP channel data characterize channel exchange flows for LSB as well as SP.

Data Analysis

Statistics were calculated in SPSS, Version 16.0 (2007). All paired t-test comparisons followed significant ANOVA results for all comparisons, where significance is determined as $p < 0.05$. Tukey's HSD was applied to all post-hoc comparisons to adjust calculations for multiple comparisons. All error estimates reported are ± 1 standard error. Lack of replication in some datasets precluded statistical analysis for the 2002 dataset.

Results

Retrospective data analysis – long-term frequency of exchange flow

The 26 years of near-shore Lake Ontario water temperature data show that there was a mean of 4.92 (± 0.29) upwelling events per year along the southern shoreline (Fig. 2.4), 2.32 (± 0.19) per year of which were longer sustained upwelling events (≥ 4 days) capable of causing significant exchange flow with the embayment. Shorter duration upwellings were about equally common (though perhaps more difficult to detect), with a mean of 1.92 (±0.29) brief, but sustained, upwellings per year. Pulsing upwellings occurred on average 0.68 (± 0.15) times per year. It appears likely, then, that exchange flows are sufficiently common to have the potential to influence the dynamics of the pelagic zone of coastal embayments on the south shore of Lake Ontario.

Retrospective data analysis – the 2002 upwelling event

The period from 20 August to 5 September 2002 was characterized by two upwelling events in Lake Ontario (Fig. 2.3a): a brief upwelling followed two days later by a sustained six-day event. Current velocity (ADCP) data taken in the SP

Figure 2.4 Number of short (<3 days), pulsing (multiple events separated by one day or less), and long (>3 days) upwelling events occurring each year along the southern LO shoreline. Events identified as periods of time during which LO surface water<15˚C during period of summer thermal stratification.

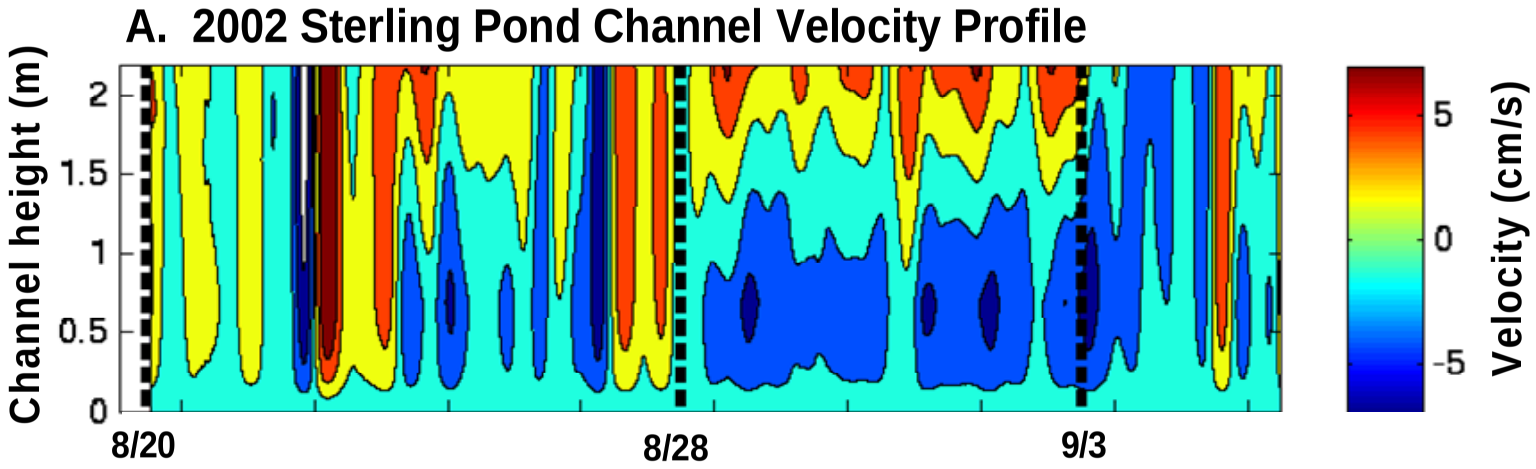
Number of events
0
1
2
3
4
5
6
7
8
9
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
short
pulsing
long

channel show that the colder LO upwelling water flowed into the embayment along the bottom of the channel while warm embayment water was displaced out along the surface of the channel for both upwelling events. There were also periods when essentially the entire channel was filled with Lake Ontario water flowing in to SP, which was followed by full-channel flow out of the embayment (e.g., 22-24 Aug., 27-28 Aug., 5 Sept.; Fig. 2.5a). The first, brief, upwelling occurred on 24 and 25 Aug. entirely between our routine sampling dates of 20 Aug. and 28 Aug., while the second event started immediately following the 28 Aug. sampling date and continued until the 3 Sept. sampling date. Temperature data indicate that water at the LO site reached its coldest temperatures during the sustained event (as low as 6.3 °C), whereas returning surface water was between 16 and 22 °C (Fig. 2.3a).

On 20 Aug., before upwelling in LO, the center site in LSB exhibited typical late-summer temperature and dissolved oxygen stratification patterns (Figs. 2.6 and 2.7). The epilimnion occupied the top 6 m of the water column, with temperature ranging between 25.9 °C and 24.0 °C. Below 6 m, the temperature decreased to 13.9 °C at the bottom (10.5 m). Mean dissolved oxygen levels were between 7 and 8 mg O_2/L throughout the epilimnion, but below 6 m, hypolimnetic oxygen levels decreased to near zero (Fig. 2.7b).

Temperature data from LO (Fig. 2.3a) and the SP channel velocity data (Fig. 2.5a) show a brief upwelling event on 24 Aug. before the longer sustained event. Rueda and Cowen (2005) found using their SI3D model that upwelling hypolimnetic LO water from this short event must have entered LSB along the bottom of the channel. However, the temperature gradient was not strong enough to force the LO water through the LSB thermocline, and instead the LO water flowed into the embayment along the thermocline, eventually mixing into the epilimnion. The LSB temperature data (Fig. 2.6) are consistent with the model, showing that the epilimnetic

Figure 2.5 Interpolated water velocity profiles through the SP channel water column during upwelling exchange-flow events in 2002 (a) and 2003 (b). Data collected by ADCP (E.A. Cowen and A.T. King, personal communication). Positive (red) values represent water moving from the embayment out into LO, while negative (blue) values represent water flow from LO into SP. Dashed lines represent embayment routine weekly (a) and event-based (b) sampling dates.


A. 2002 Sterling Pond Channel Velocity Profile
Channel height (m)
2
1.5
1
0.5
0
8/20
8/28
9/3
5
0
-5
Velocity (cm/s)

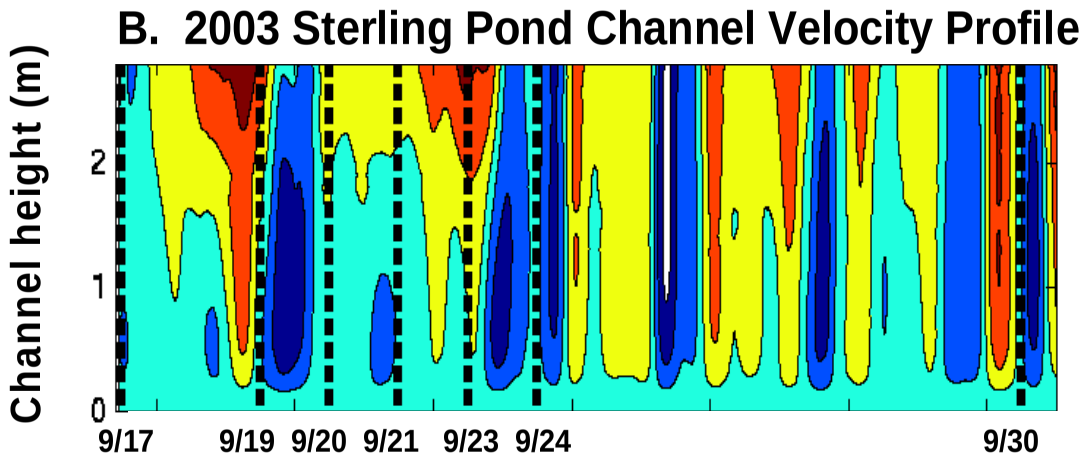
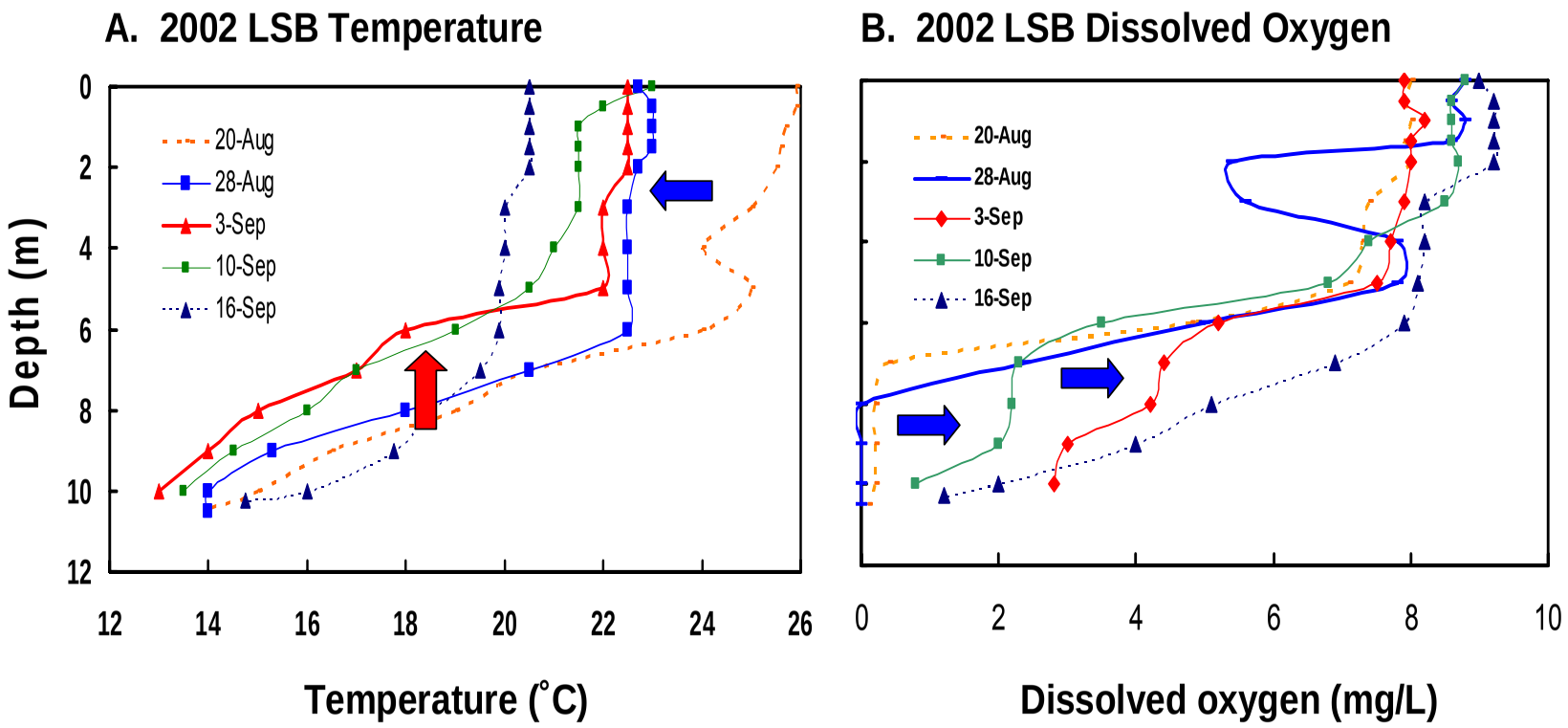

B. 2003 Sterling Pond Channel Velocity Profile
Channel height (m)
2
1
0
9/17
9/19
9/20
9/21
9/23
9/24
9/30

Figure 2.6 Interpolated 2002 time-depth temperature profiles in LSB center site water column. Thermister strings set at one meter intervals recorded data continuously (1 hour increments) from surface to bottom. Dashed lines represent routine weekly sampling dates (E.A. Cowen and A.T. King, personal communication).

Degrees C
25
20
15
10
Depth (m)
2
4
6
8
10
8/20
8/28
9/3

Figure 2.7 2002 temperature (a) and dissolved oxygen (b) profiles at LSB center site. Dashed profile lines represent pre- and post event sampling dates; solid profiles are during events. Arrows indicate direction of strong changes between dates.


A. 2002 LSB Temperature
Depth (m)
0
2
4
6
8
10
12
20-Aug
28-Aug
3-Sep
10-Sep
16-Sep
12
14
16
18
20
22
24
26
Temperature (˚C)
B. 2002 LSB Dissolved Oxygen
20-Aug
28-Aug
3-Sep
10-Sep
16-Sep
0
2
4
6
8
10
Dissolved oxygen (mg/L)

stratification began to break down between 20 and 28 Aug. Temperature profile data also show that the entire epilimnion cooled by 1.5 to 3.2 °C during this period, while the hypolimnion remained at essentially a constant temperature (Fig. 2.7). Dissolved oxygen in the hypolimnion also remained constant (although the oxycline deepened by almost a meter), while the epilimnion showed an increase in dissolved oxygen of almost 1 mg/L (except for an unexplained marked negative heterograde pattern in the surface waters on 28 Aug.: Fig. 2.7b).

The LO thermistor data (Fig. 2.3a) show the sustained upwelling event beginning on 28 August. Rueda and Cowen's (2005) simulation depicts the cold hypolimnetic LO water flowing along the bottom of the channel into LSB and then flowing down the basin slope to the bottom of the embayment, where it fills the system from the bottom up, forcing the warmer LSB epilimnetic water out through the top of the channel. Our temperature data show that the incoming hypolimnetic water was cooler (8 - 10 °C) than the hypolimnetic LSB water (~13 °C), and so did not thoroughly mix with it, but instead displaced the LSB hypolimnion up higher into the water column. During this period, SP channel velocity data show the water beginning to flow into the SP embayment along the bottom of the channel, accompanied by a bi-directional flow of water moving at the channel surface from the embayment out into L. Ontario (Fig. 2.5a). Bi-directional flow continued in a sustained manner throughout the week of 28 Aug. to 3 Sept. On 29 Aug., LSB thermistor data from the center site show cold water filling in along the bottom of the embayment, and the thermocline ultimately being displaced upwards by over 2 m (Fig. 2.6).

Temperature profile data from the LSB center site (Fig. 2.7a) also show the temperature in the top 5 m of the water column only decreasing slightly (0.2 - 0.5 °C) over the course of the week while temperature in the bottom 4 m decreased by 1.0 to 4.5 °C as the LO water intruded. The most extreme temperature change occurred at 6

– 8 m, the depth of the thermocline when the event started, as cold water intruded higher into the water column (Fig. 2.7a). Accompanying these temperature changes in deep LSB water was a large increase in dissolved oxygen of as much as 4.2 mg O_2/L in the previously anoxic bottom four meters of the embayment (Fig. 2.7b). By 3 Sept., LO thermistor data suggest that the upwelling event was ending, however, the LO water column remained filled with cooler, ~15 °C water. SP channel velocity data show that cool LO water is barotropically forced into the embayment, filling the SP water column from top to bottom with LO water, followed by a corresponding flow of embayment water back out into LO as warm water returned to the near-shore of LO (Fig. 2.5a).

2003 and 2004 short-term upwelling event sampling

Physical comparison of upwellings in both events

The inland excursion across New York State of two hurricanes, Isabel in September 2003 and Francis in September 2004, provided opportunities to anticipate upwelling events in LO and to follow their effects on exchange flows in LSB and SP. As Hurricane Isabel moved north over LO on 19 Sept. 2003, we documented two approximately 36-h periods (separated by a 12-24 hour interval) during which upwelled cold hypolimnetic water filled the near shore water column. The coldest water (< 10 °C) was detected during the second pulse (Fig. 2.3b). Channel velocity data from the SP channel (and complementary temperature probe data in LSB channel) show that this cold water flowed in through the channels of both embayments, filling them from bottom to top for about 12 h on both occasions (Fig. 2.5b). Bi-directional exchange flow, with colder LO water flowing into the embayment along the bottom of the channel and warmer embayment water flowing

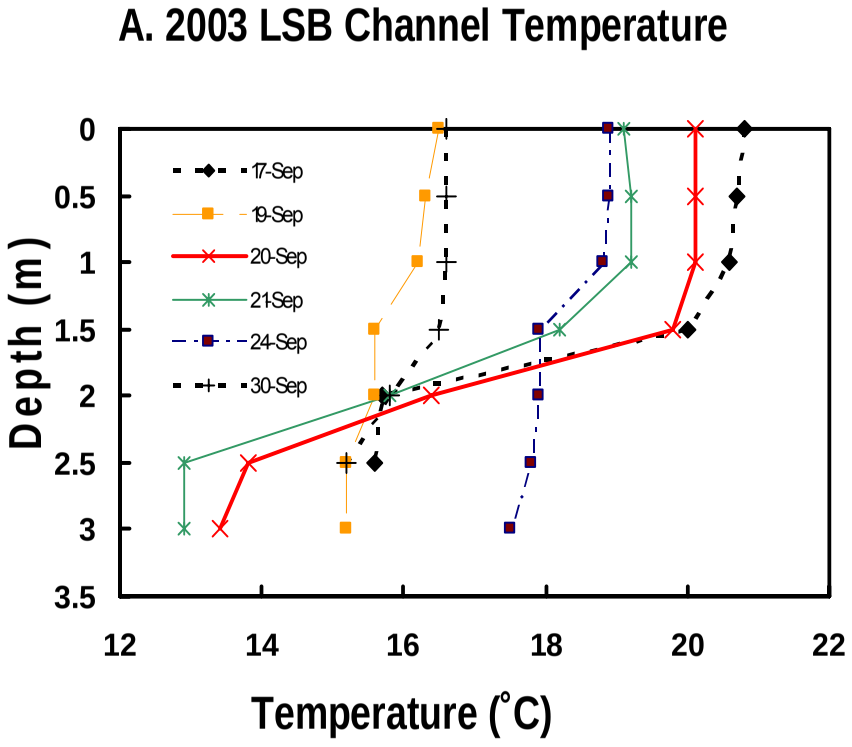
out the top of the channel, occurred in both channels between these larger pulses of hypolimnetic LO water.

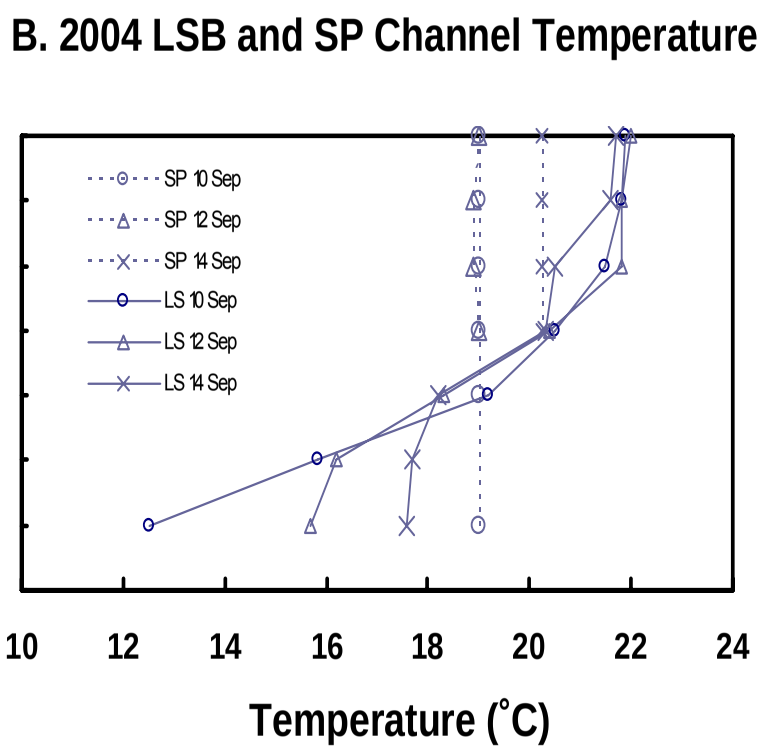
As Hurricane Frances crossed New York State and over LO on 9 September 2004, the upwelling event it caused near LSB and SP differed from the 2003 event in that the cold, upwelled hypolimnetic water remained consistently up along the LO shoreline for a sustained period of approximately 84 h (Fig. 2.3c). A strong temperature gradient, indicative of bi-directional flow was detected in the LSB channel, with 12.5 °C water flowing into the embayment along the bottom of the channel and 21 °C water flowing out along the top of the channel on 10 Sept. (Fig. 2.8b). This was notably not the case in the SP channel, which contained only warm (18-20 °C) water filling the channel throughout the course of the event (Fig. 2.8b). This difference among years and embayments is explained by the fact that unlike the 2003 event, which did not have precipitation associated with it, the 2004 event was accompanied by heavy rainfall and a flow rate in the Sterling Creek tributary to SP that increased from virtually no flow on 7 Sept. to 7 $m^3 s^{-1}$ by 9 Sept. (Fig. 2.9). The flow rate gradually decreased throughout the LO upwelling event, but did not fall below 2 $m^3 s^{-1}$ until after the upwelling event had concluded. Heavily tannin-stained water visibly flowed from the creek, through the embayment, out of the channel and into near-shore LO throughout the event, carrying many pieces of broken macrophyte stems and leaves. Due to its small watershed and tributary, there was no comparable effect of storm runoff in LSB in 2004.

2003 Lake Ontario upwelling response summary

Both thermistor-string data (Fig. 2.4b) and temperature-probe data (Fig. 2.10a) show that the near-shore LO site was 10 to 14 °C from top to bottom during both upwelling surges in 2003 and that dissolved oxygen was super-saturated during the

Figure 2.8 LSB (a) and SP (b) channel temperature profiles in 2003 (LSB) and 2004. Dashed profile lines in (a) represent pre- and post event sampling dates; solid profiles are during events. Dashed profile lines in (b) represent SP samples; solid profiles are LSB samples.


A. 2003 LSB Channel Temperature
Depth (m)
0
0.5
1
1.5
2
2.5
3
3.5
12
14
16
18
20
22
Temperature (˚C)
17-Sep
19-Sep
20-Sep
21-Sep
24-Sep
30-Sep


B. 2004 LSB and SP Channel Temperature
10
12
14
16
18
20
22
24
Temperature (˚C)
SP 10 Sep
SP 12 Sep
SP 14 Sep
LS 10 Sep
LS 12 Sep
LS 14 Sep

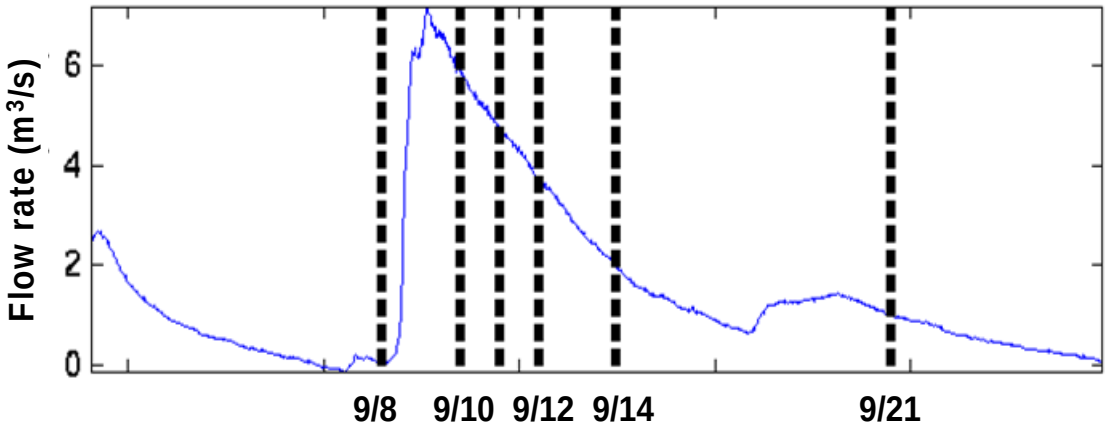
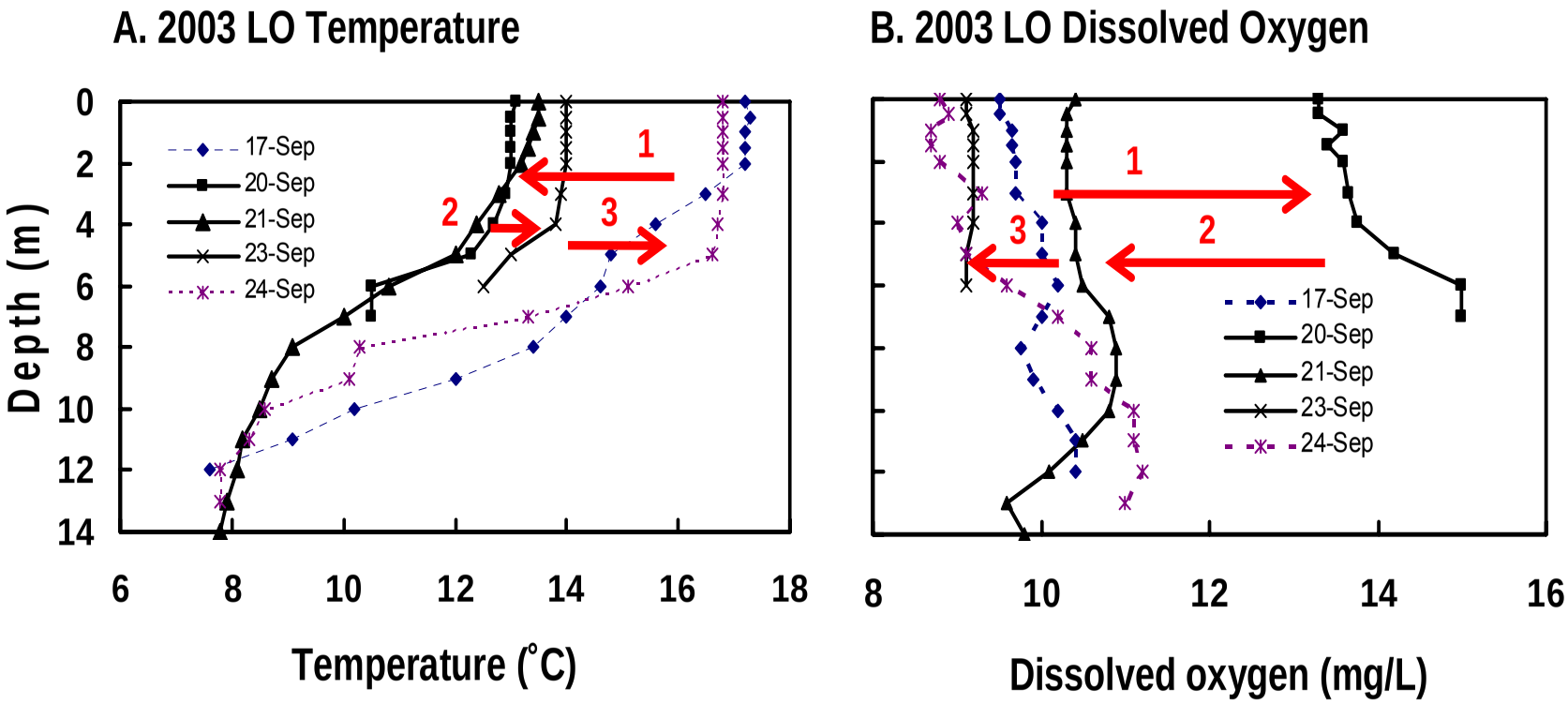


Figure 2.9 Sterling creek flow rate during 2004 upwelling event (Cornell University 2010). Dashed lines represent upwelling event sampling dates.

Figure 2.10 2003 temperature (a) and dissolved oxygen (b) profiles at LO near-shore sampling site. Dashed profile lines represent pre- and post event sampling dates; solid profiles are during events.


A. 2003 LO Temperature
Depth (m)
0
2
4
6
8
10
12
14
6
8
10
12
14
16
18
Temperature (˚C)
17-Sep
20-Sep
21-Sep
23-Sep
24-Sep
1
2
3
B. 2003 LO Dissolved Oxygen
8
10
12
14
16
Dissolved oxygen (mg/L)
17-Sep
20-Sep
21-Sep
23-Sep
24-Sep
1
2
3

first surge (14-15 mg L^{-1}), but decreased down to pre-event levels (9-10 mg L^{-1}) during the course of the event (Fig. 2.10 a-b). Near-shore pre-event (17 Sept.) zooplankton densities showed a marked temporal pattern of vertical distribution with abundance at 2.5 m ten-fold greater than that at 6.5 m (Fig. 2.11a)**.** In contrast, during the event (21 Sept.), zooplankton densities became uniform with values comparable to those pre-event at 6.5 m, consistent with an interpretation that the entire water column was filled with upwelling hypolimnetic water. The original zooplankton distribution, with density greater near the surface, was reestablished once the upwelling event ended on 24 Sept. (Fig. 2.11a, 2-m density significantly greater than 6.5-m density pre- and post- event: t-test**,** df = 2; 17 Sept.: t = 127.46, p = 0.0025; 24 Sept.: t = 25.02, p = 0.013; NS during the event 21 Sept.: t = 0.27, p = 0.415).

Cladocerans declined significantly from pre-event biomass values (Fig. 2.12, paired t-test, df = 1, t = 13.047, p = 0.024) while copepods did not change significantly in total biomass. The zooplankton showed a significant biomass increase post-event relative to the pre-event surface water density (Fig. 2.11a, t-test, df = 1, t = 10.59, p = 0.03). This increase was due primarily to cladocerans, particularly *Daphnia retrocurva* and *Bosmina longirostris*, which both changed significantly in abundance through the event (one-way ANOVA, df = 2, *D. retrocurva* F = 166.130, p = 0.001; *B. longirostris* F = 44.409, p = 0.006; all post-hoc comparisons for both species $p < 0.05$, except *B. longirostris* 17 Sept. vs. 21 Sept., p = 0.073).

Total phytoplankton biovolume in near-shore LO followed a similar, albeit not statistically significant, trend of decreasing in the surface during the event and increasing post-event (Fig. 2.11b). There were no significant differences among dates and depths presumably due to high variance in the 17 Sept. and 24 Sept. samples from 2 m (ANOVA, df = 5, F = 2.870, p = 0.116). During the event, the phytoplankton community had a significantly higher percentage of edible taxa than before and after

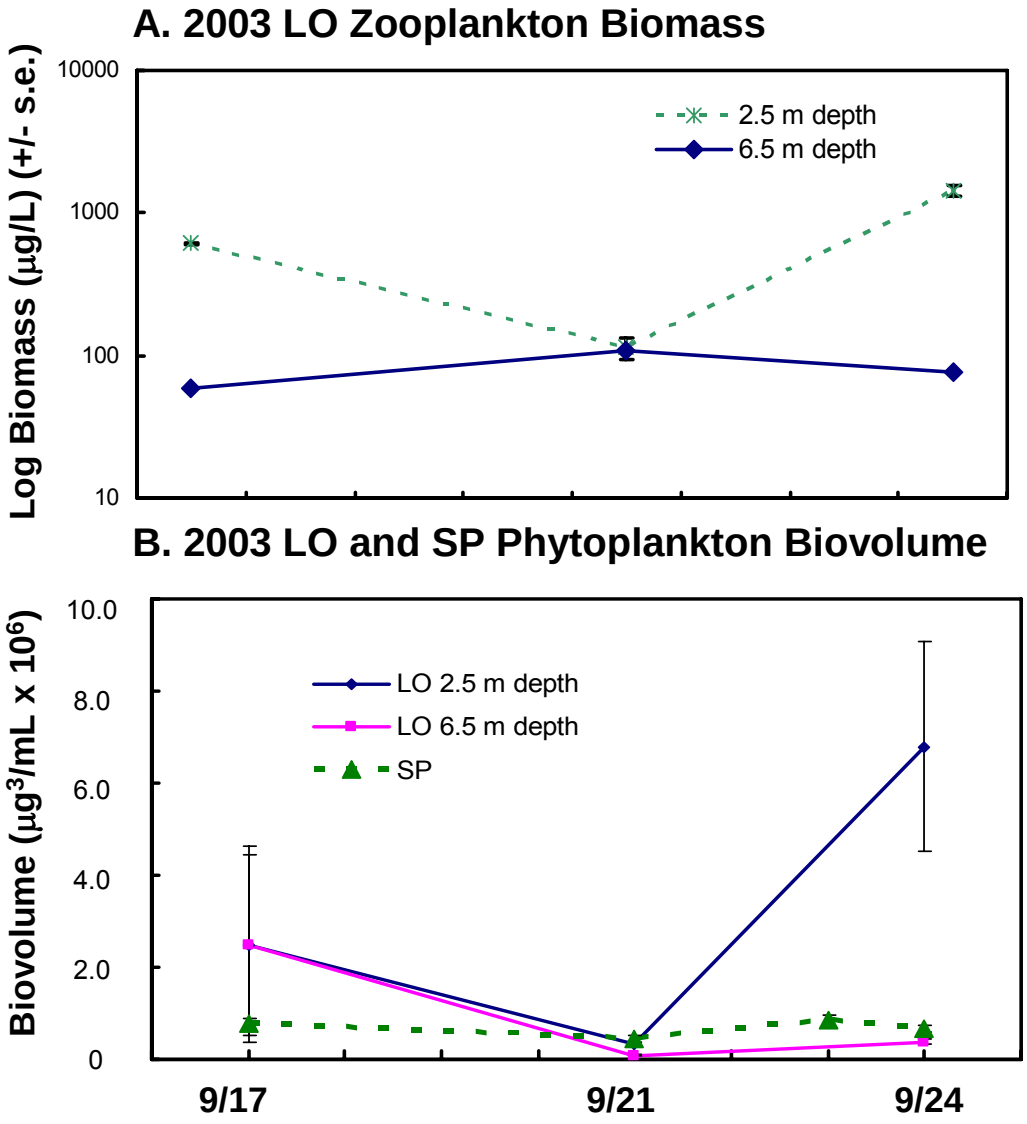


Figure 2.11 2003 zooplankton biomass (a) and phytoplankton biovolume (b) at near-shore LO sampling site before (17 Sept.), during (21 Sept.), and after (24 Sept.) upwelling event. SP phytoplankton (dashed line) added for comparison (b). Error bars represent 1 s.e.

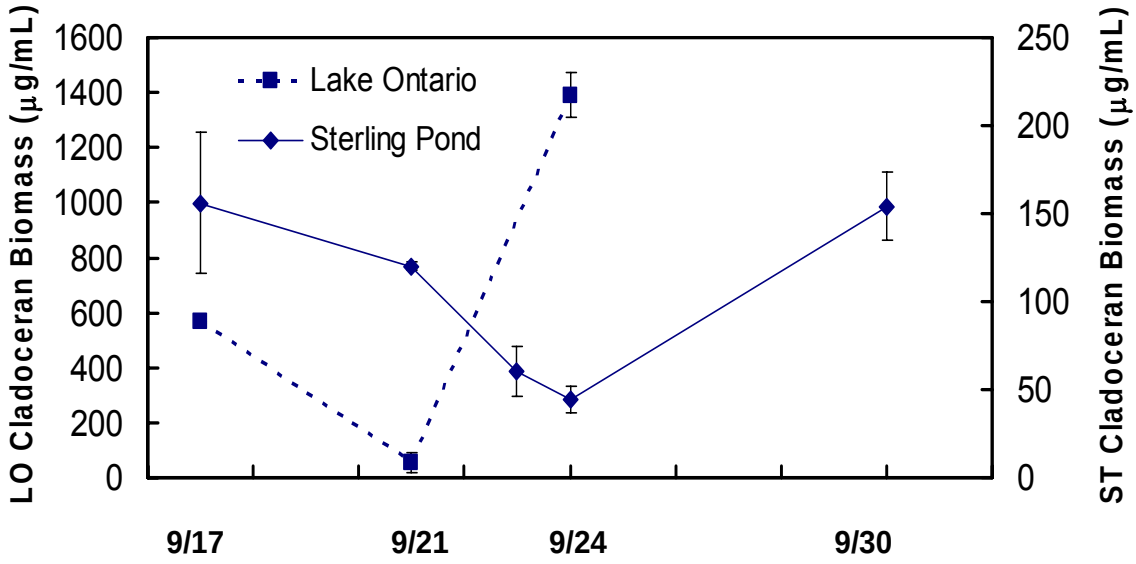


Figure 2.12 LO and SP cladoceran biomass before (17 Sept.), during (21, 23 Sept.), and after (24, 30 Sept.) 2003 upwelling event. Error bars represent 1 s.e.

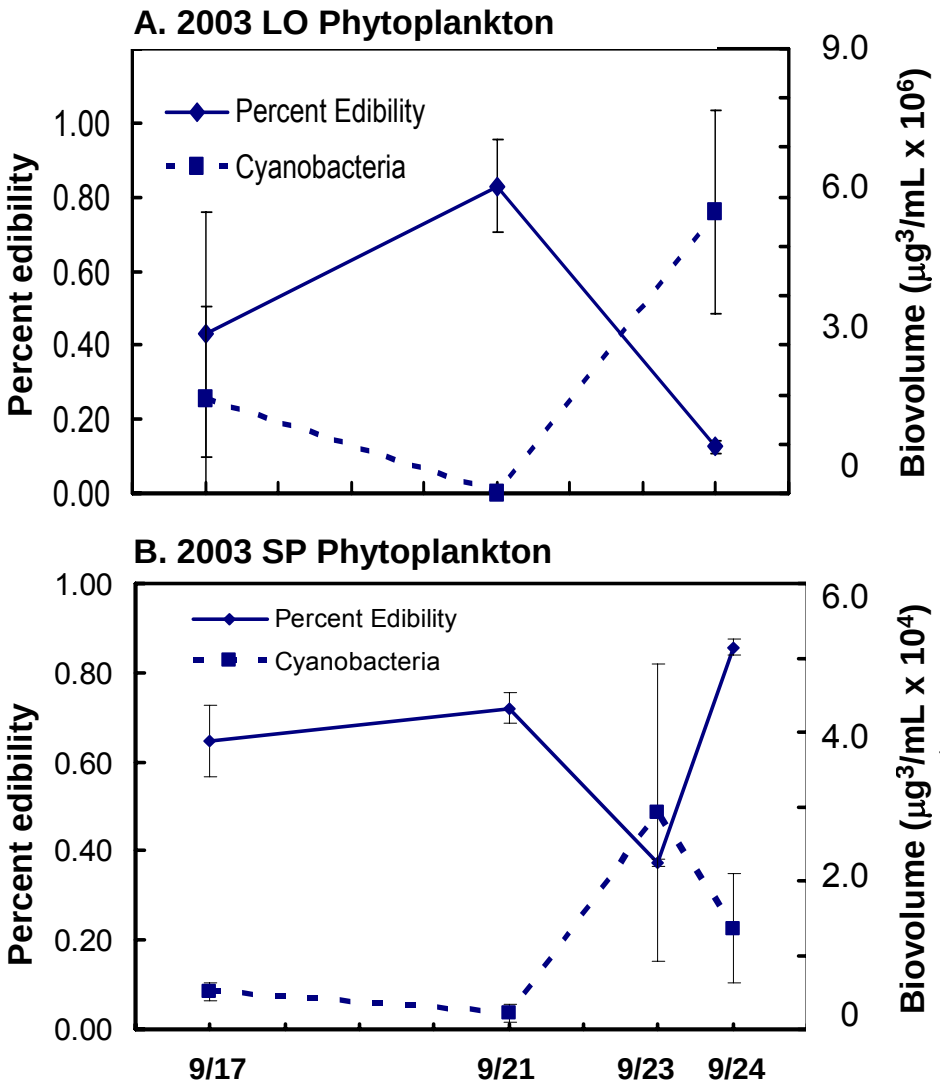


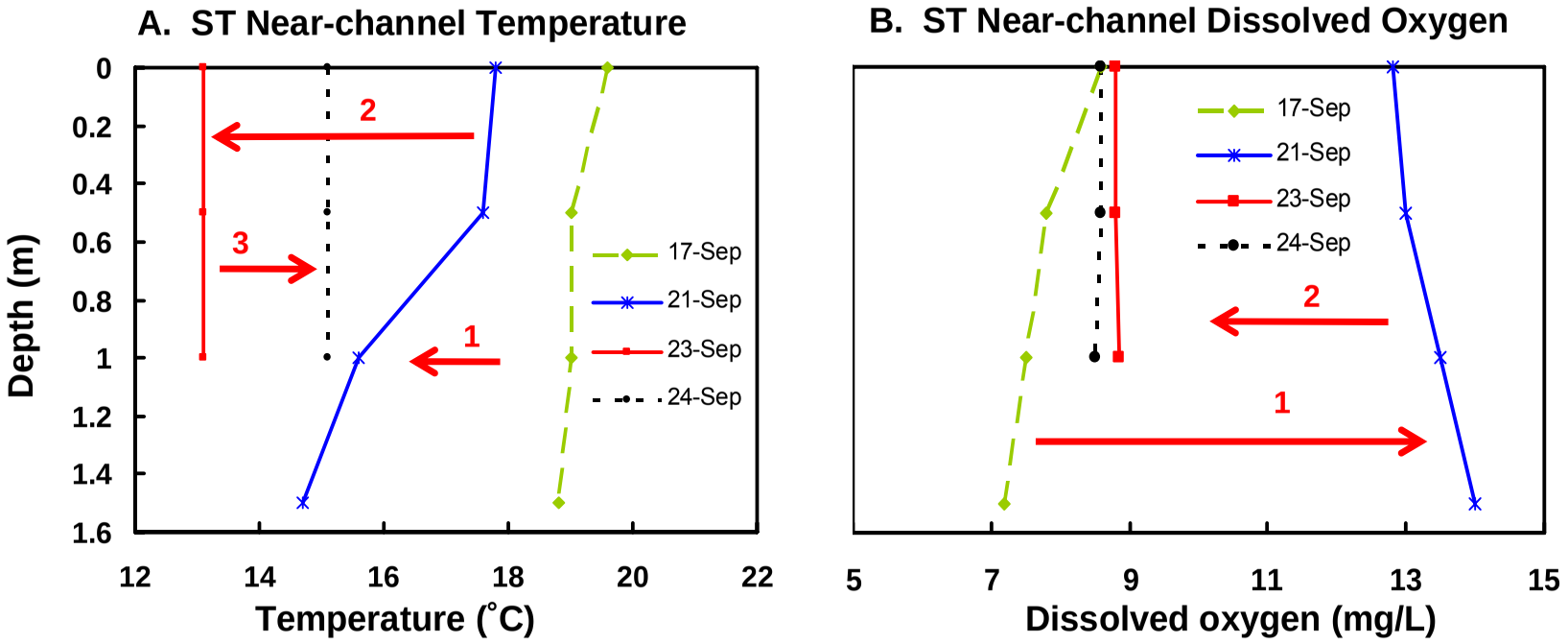
Figure 2.13 2003 LO (a. near-shore sampling site) and SP (b. near-channel site) phytoplankton edibility and cyanobacteria dynamics. Error bars represent 1 s.e.

the upwelling (Fig. 2.13a, t-test, df = 4, t = 2.69, p = 0.027). Two taxa not previously present appeared during this time, *Asterionella* sp. and *Peridinian* sp., while all other taxa present pre-event either disappeared or decreased in numbers. The increase in edibility was driven by the marked decrease in cyanobacteria, particularly *Anabaena,* which disappeared altogether during the event before reappearing post-event (Fig. 13a). The apparent post-event increase in phytoplankton biovolume was driven most strongly by increases of small edible *Cryptomonas, Sphaeorcystis,* and microflagellate species, as well as colonial species such as *Coelastrum reticulatum* and *Fragilaria sp.* and the mixotroph *Ceratium hirundinella.*

2003 Embayment response dynamics

Vertical profiles of temperature and dissolved oxygen measured throughout the 2003 upwelling event in SP showed clear evidence of cold, highly oxygenated upwelling water appearing at the near-channel SP site only (Fig. 2.14). A plug of cold, highly oxygenated water flowing into SP during the event was traced from the channel through the embayment using a probe deployed from our boat. It flowed through the open-water near-channel site and to the dense bed of macrophytes surrounding the center site, but could not be tracked into the rooted plants and was not detected at the center site. Temperature profiles taken at the near-channel SP site before the event showed the water column was filled from top to bottom with 19 °C water. Following the first pulse of upwelled water along the LO shoreline (19 Sept.), the bottom half-meter of water at the SP near-channel site became filled with 15 °C water while surface water remained only slightly cooler than pre-event. The second pulse of upwelling water on 23 Sept. filled the near-channel site with 13 °C water

Figure 2.14 2003 temperature (a) and dissolved oxygen (b) profiles at SP near-channel sampling site. Dashed profile lines represent pre- and post event sampling dates; solid profiles are during events. Arrows indicate direction of strong changes between dates.


A. ST Near-channel Temperature
Depth (m)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
12
14
16
18
20
22
Temperature (˚C)
2
3
1
17-Sep
21-Sep
23-Sep
24-Sep
B. ST Near-channel Dissolved Oxygen
5
7
9
11
13
15
Dissolved oxygen (mg/L)
17-Sep
21-Sep
23-Sep
24-Sep
2
1

from bottom to top. Dissolved oxygen levels tracked those seen in LO during these two intrusions (cf. Figs. 2.10b and 2.14b). Although no such change was measured at our near-channel or center sampling sites in LSB, we were able to trace the cold, high DO water flowing from the channel into the embayment on 21 Sept. 2003 using a probe deployed from a boat. A narrow and vertically thin stream bypassed the near-channel site to the east, following the deepest contour of the embayment bottom out into the embayment (Fig. 2.2) to a depth at which point it could no longer be detected in the rough weather.

Plankton populations in SP (near channel) also changed rapidly during the exchange flow event. Both phytoplankton and zooplankton showed marked changes between 17 Sept. (pre-event) and 23 Sept. (peak of second event; plankton not sampled on 19 Sept.). Phytoplankton biovolume mimicked that in LO, decreasing following the first upwelling pulse to a level that did not statistically differ from LO surface phytoplankton biovolume on 21 Sept. (Fig. 2.15a, t-test, df = 1, t = 2.81, p = 0.11). The community then rebounded during the second pulse on 23 Sept., driven by an increase in the inedible phytoplankton group, which changed significantly in total biovolume throughout the event (Fig. 2.15a, one-way ANOVA, df = 7, F = 17.98, p = 0.009; Tukey's HSD 21 Sept. vs. 23 Sept.: p = 0.012). Unlike LO, edible species did not change significantly in total biovolume during the event (one-way ANOVA, df = 3, F = 2.537, p = 0.195), including during this time period (Tukey's HSD p = 0.999), which led to increased overall inedibility of phytoplankton on 23 Sept. (Fig. 2.13b). This increase in inedibility was driven in part by increases in cyanobacteria, especially *Anabaena* sp. and *Oscillatoria* sp., which had disappeared during the upwelling in LO (Fig. 2.13a-b). Immediately following the event (24 Sept.), overall phytoplankton biovolume was not significantly different from pre-event values, however community composition was not the same as edibles had not changed (Tukey's HSD p = 0.266),

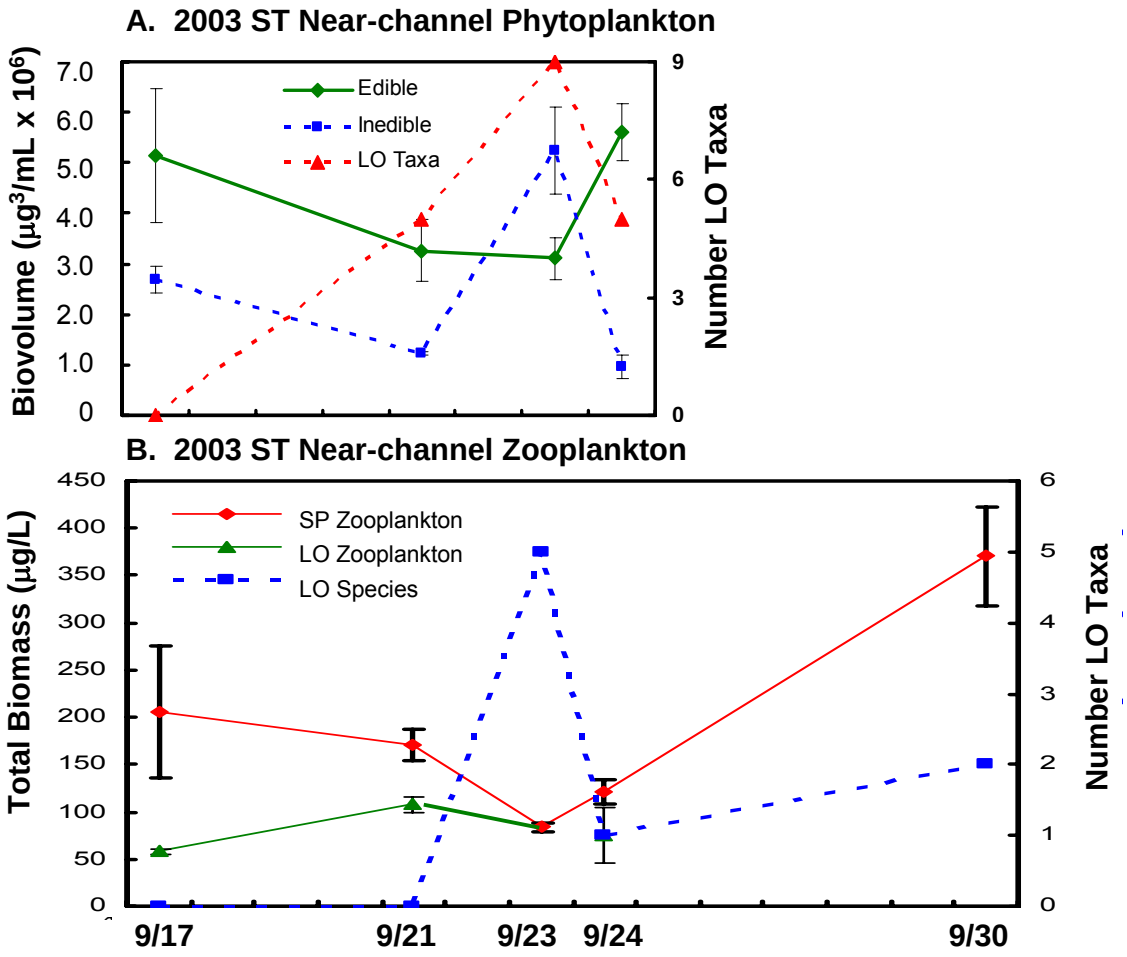


Figure 2.15 2003 phytoplankton biovolume (a) and zooplankton biomass (b) at near-channel SP sampling site before (17 Sept.), during (21 and 23 Sept.), and after (24 Sept.) upwelling event. Error bars represent 1 s.e.

while inedibles decreased significantly from 23 Sept. to a level comparable to pre-event conditions (Fig. 2.15a, Tukey's HSD $p = 0.010$, $p = 0.174$ respectively). Total zooplankton biomass also changed significantly in SP (near-channel site) over the course of the event (Fig. 2.15b, one-way ANOVA, $df = 4$, $F = 15.16$, $p = 0.005$). While we did not see a notable decrease after the first pulse (21 Sept.), total biomass appeared to decline by about half from pre-event values after the second upwelling pulse, though the change was not significant (23 Sept., Tukey's HSD $p = 0.131$). The resulting biomass value mirrored zooplankton density in near-shore LO on 21 Sept., with no significant difference in total biomass between the two locations (t-test, $df = 1$, $t = 2.062$, $p = 0.144$). Post-hoc tests showed SP zooplankton biomass increased to levels significantly greater than all other dates after the exchange event ended (e.g., Tukey's HSD post-hoc test comparing pre- and post-event biomass, $p = 0.048$). As in LO, this post-event increase was driven predominantly by the cladoceran population. Cladocerans followed a similar trajectory to that in LO, but delayed by several days, decreasing through the event and increasing to significantly greater biomass following the event (Fig. 2.12, ANOVA, $df = 4$, $F = 34.342$, $p = 0.001$; post-hoc comparison 30 Sept., $p \leq 0.004$ for all comparisons). The cladocerans *Ceriodaphnia* spp. and *Chydorus sphaericus* disappeared from both sites with the influx of upwelling water. While *Daphnia mendotae* made up much of the post-upwelling cladoceran increase in LO (comprising 80% of 24 Sept. biomass), *Bosmina longirostris* reached significantly greater densities than seen before the event in SP (paired t-test, $df = 1$, $t = 8.33$, $p = 0.038$), comprising the largest portion (54 %) of the total biomass on 30 Sept.

Most strikingly, plankton taxonomic composition showed a strong influence of the intrusion of LO water into SP. Eleven LO phytoplankton taxa that had not previously been found in SP in 2003 appeared on 21 and 23 Sept., following the two

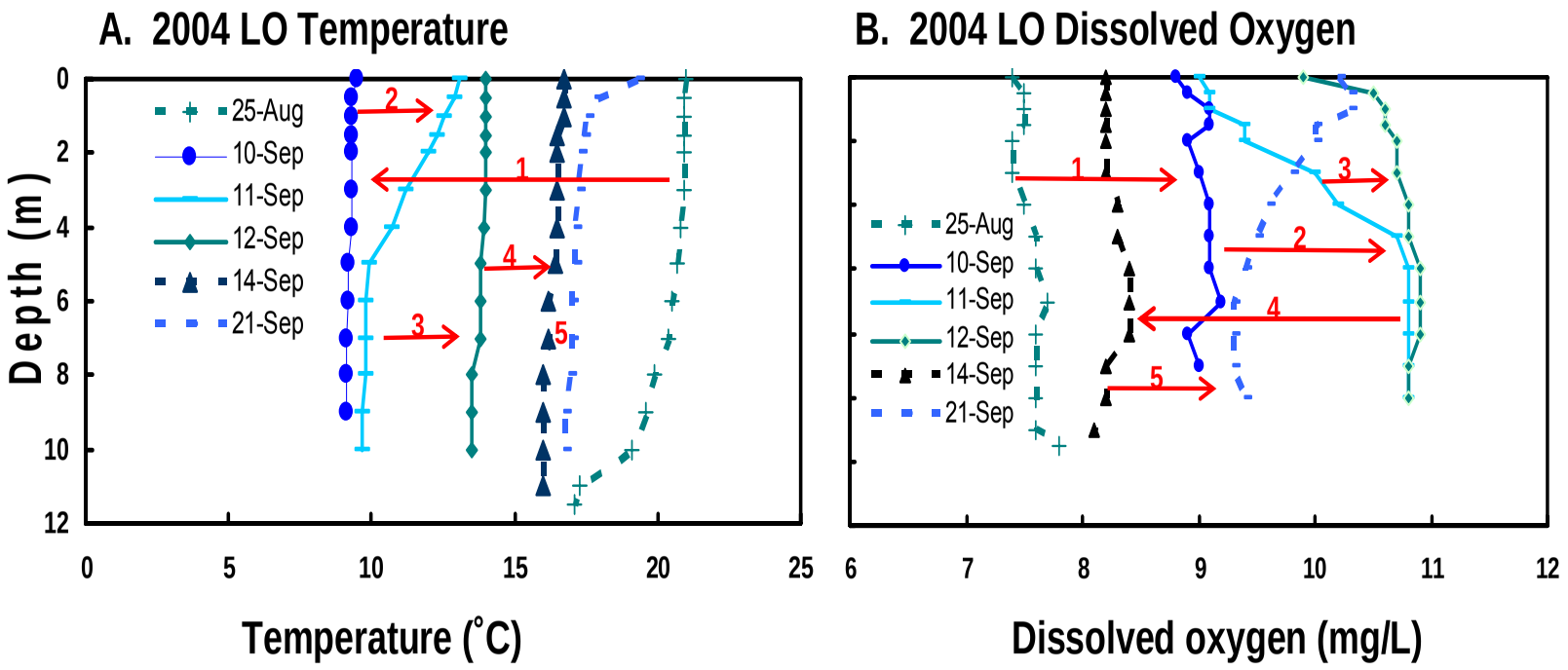
exchange events (Fig. 2.15a), including species from four distinct higher taxa: Chlorophyta, Bacillariophyta, Pyrrophyta, and Cyanobacteria. Five zooplankton taxa novel to SP, but present in LO, also appeared in SP on this date, including three rotifer species, plus *Daphnia retrocurva*, and *Cercopagis pengoi*. Two of these phytoplankton taxa (*Anabaena* sp. and *Merismopedia* sp.) and two of the rotifers (*Kellicotia* sp. and *Keratella* sp.) were also found in SP after the event, as was the predatory cladoceran *Cercopagis*, which was detected again on the last day of sampling (30 Sept.), one week post-event (Fig. 2.15b), indicating that at least some of the LO taxa persisted for an extended period after the upwelling event.

2004 Lake Ontario upwelling response

Vertical temperature profiles collected throughout the 2004 event in near-shore LO (Fig. 2.16a) were consistent with the thermistor data (Fig. 2.3c), showing the water column decreasing by about 10 °C from pre-event to the first sampling day after the start of upwelling (10 Sept.), along with an associated increase in dissolved oxygen (Fig. 2.16b). On the second day of the upwelling (11 Sept.), LO temperature and dissolved oxygen were both stratified, with the surface water slightly warmer than the previous day, and the water increasing substantially in dissolved oxygen with depth. By the third day of the event (12 Sept.) the water column had returned to being unstratified (13.5-14 °C) with high dissolved oxygen (10 - 11 mg O_2 L^{-1}). The near-shore LO water column gradually moved back to pre-event conditions over the course of the following week (Figs. 2.16a-b).

Total phytoplankton biovolume in near-shore LO varied significantly over the course of the event, when compared among all dates and depths sampled, (ANOVA, $df = 19$, $F = 27.085$, $p < 0.001$). These patterns were driven exclusively by significantly greater phytoplankton biovolume in the post-event (24 Sept.) surface

Figure 2.16 2004 temperature (a) and dissolved oxygen (b) profiles at LO near-shore sampling site. Dashed profile lines represent pre- and post event sampling dates; solid profiles are during events. Arrows indicate direction of strong changes between dates.


A. 2004 LO Temperature
Depth (m)
0
2
4
6
8
10
12
0
5
10
15
20
25
Temperature (˚C)
25-Aug
10-Sep
11-Sep
12-Sep
14-Sep
21-Sep
1
2
3
4
5
B. 2004 LO Dissolved Oxygen
6
7
8
9
10
11
12
Dissolved oxygen (mg/L)

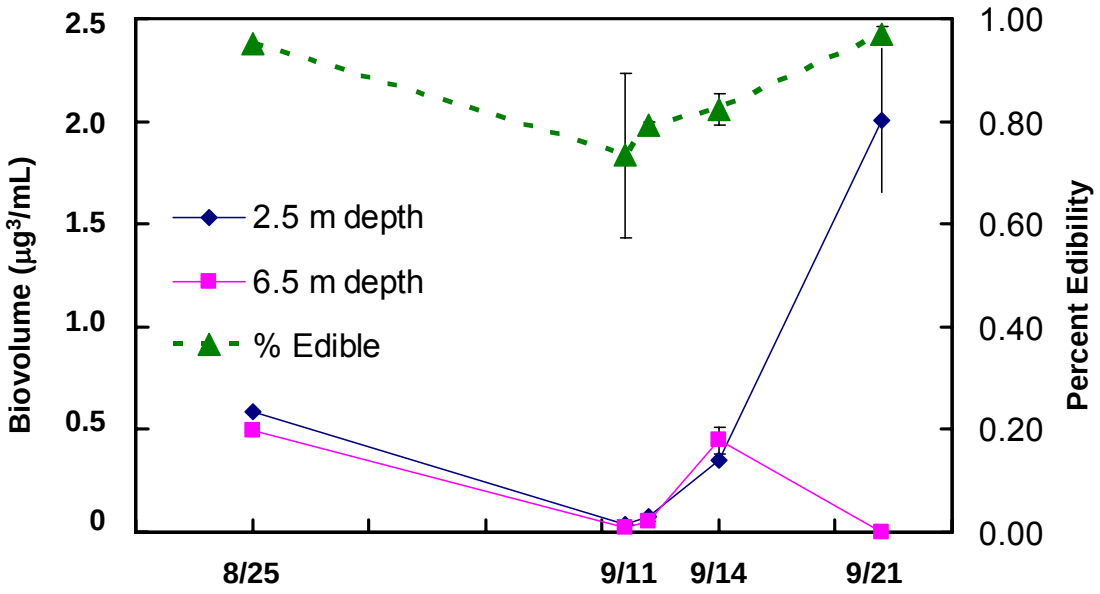


Figure 2.17 2004 LO near-shore site phytoplankton biovolume at shallow and deep depths and % edibility (combined depths). Error bars represent 1 s.e.

water samples than in the surface or deep waters on all other dates (Fig. 2.17, Tukey's HSD, $p < 0.001$ for all comparisons). Total phytoplankton biovolume was not significantly different at either 2.5 m or 6.5 m pre-event, and the apparent decrease in phytoplankton at both depths from pre-event conditions in late August to the first day of upwelling was not statistically significant (10 Sept.; Fig. 2.17, Tukey's HSD $p = 0.109$, $p = 0.198$ for surface and deep water respectively). While percent edibility did not vary throughout the event, perhaps due to high variance among replicate samples (ANOVA df = 9, F = 1.941, p = 0.242), the community trended to be slightly less edible during the event (Fig. 2.17) with the loss of small coccoid taxa and cryptophytes like *Chroomonas.* significantly different at either 2.5 m or 6.5 m pre-event, and the apparent decrease in phytoplankton at both depths from pre-event conditions in late August to the first day 2.17). This increase in biovolume was accompanied by an increase in a number of taxa, with the greatest increases from pre-event conditions seen in *Chroomonas* sp., *Cryptomonas* sp., microflagellates, and *Aphanocapsa* sp.

Zooplankton density (data not shown) was also low during the event throughout the water column (20.19 ± 7.31 μg L^{-1} average biomass; no difference between depths: t-test, df = 1, t = 0.11, p = 0.47), but began to increase on 14 Sept. following the event, with the surface waters containing twice the biomass of the deep waters (410.47 μg L^{-1} total biomass at 2.5 m; 191.95 μg L^{-1} total biomass at 6.5 m). Copepods were the dominant contributor to zooplankton biomass during the event, but the apparent increase following the event was primarily due to the cladocerans, particularly *Eubosmina coregoni, Holopedium gibberum.,* and *Daphnia* spp. (10 Sept. vs. 14 Sept. biomass, marginally significant increase in cladocerans: t-test, df = 7, t = 1.41, p = 0.10; no difference in copepods).

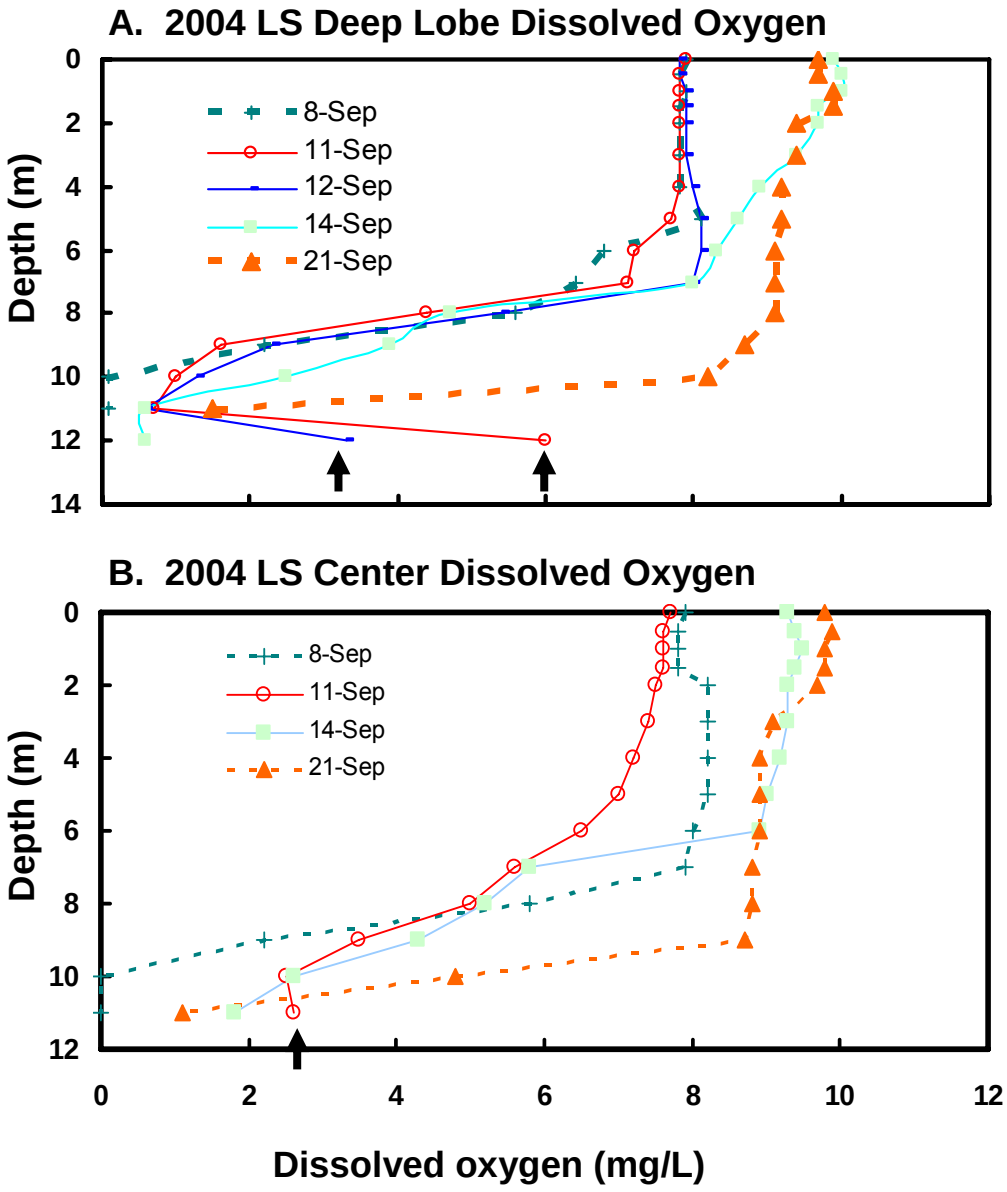


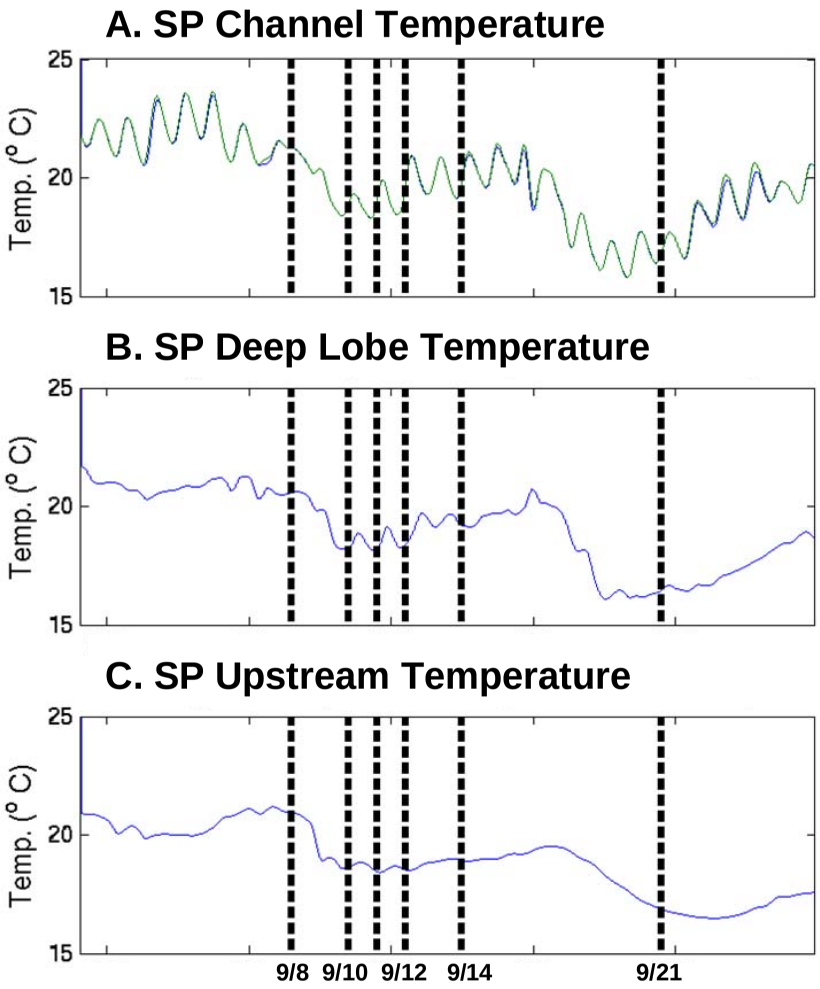
Figure 2.18 2004 LSB deep lobe (a) and center (b) site dissolved oxygen profiles. Dashed profile lines represent pre- and post event sampling dates; solid profiles are during events. Arrows indicate large increases in hypolimnetic D.O.

2004 Embayment response dynamics

Dissolved oxygen profiles at LSB, taken throughout the 2004 growing season, showed a sudden increase in oxygen levels in the bottom two meters of the LSB Deep Lobe and Center sites during the September upwelling event (Fig. 2.18 a-b), while temperature (data not shown) did not change. Pre-event hypolimnetic conditions were nearly anoxic at both sites on 25 Aug. (0.2 mg L^{-1} at 12 m and 11 m respectively) and 8 Sept. (0.1 mg L^{-1} and 0.0 mg L^{-1} respectively at 11 m), but oxygen levels increased to almost 3 mg L^{-1} in the bottom waters of the Center site, and up to 6 mg L^{-1} at the Deep Lobe site during the upwelling event (11 Sept.: Fig. 2.18 a-b). After this date, dissolved oxygen values gradually decreased in the bottom water of both sites through the rest of the upwelling event. The oxycline deepened by about a meter at both sites from before to after the event (Fig. 2.18 a-b) and neither site returned to completely anoxic conditions for the remainder of the season. Plankton sampled further up in the water column did not show a significant response to this influx of water (data not shown).

All measured variables in SP showed similar dynamics among sites throughout the 2004 event. Thermistor strings deployed in Sterling Creek, the Sterling Channel, and in the SP Deep Lobe site all showed similar temperature changes and none showed an influx of cold, upwelling water. Rather, all showed the inflow of slightly cooler stream water throughout the embayment and out through the channel (Fig. 2.19). Temperature and dissolved oxygen vertical profile data, taken throughout the event at all sites, are consistent with this interpretation. There was no vertical stratification at any site, nor was there any indication of cold, oxygen-rich upwelling LO water in SP. There was, however, strong stratification at the LO site immediately outside of SP channel, where cold, highly oxygenated water was present in the bottom half of the near-shore water column while water close in temperature and dissolved

Figure 2.19 Continuous thermister temperature measurements throughout 2004 upwelling and precipitation events at three locations in or near SP. Dashed lines represent event sampling dates (E.A. Cowen and A.T. King, personal communication).


A. SP Channel Temperature
Temp. (° C)
25
20
15
B. SP Deep Lobe Temperature
Temp. (° C)
25
20
15
C. SP Upstream Temperature
Temp. (° C)
25
20
15
9/8
9/10
9/12
9/14
9/21

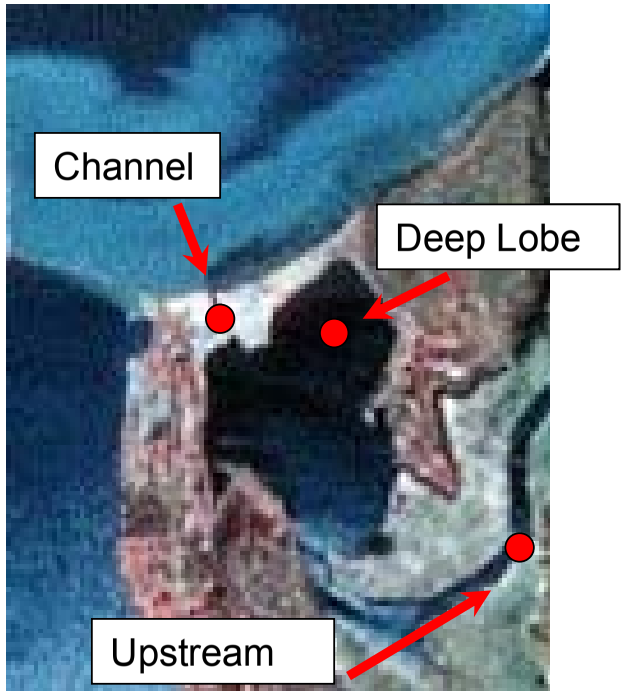
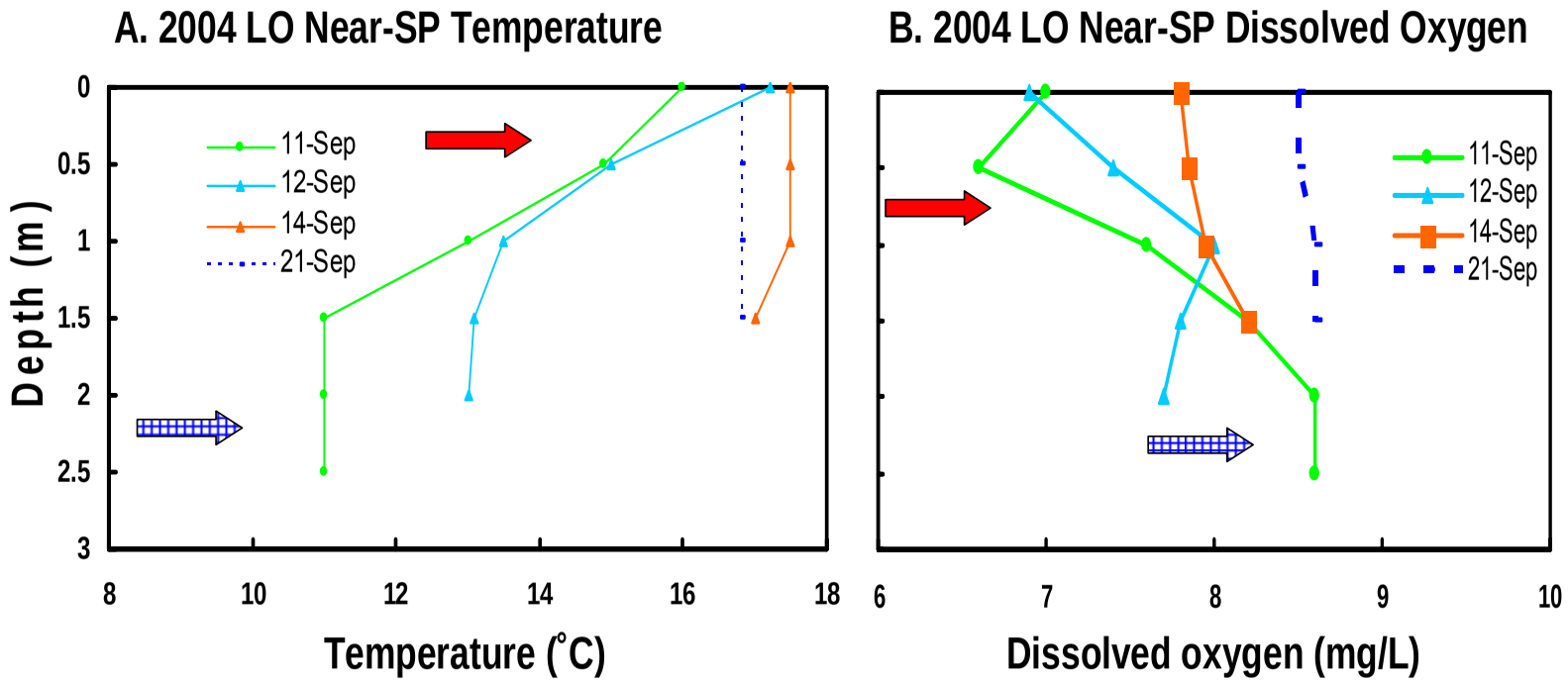

Channel
Deep Lobe
Upstream

Figure 2.20 2004 temperature (a) and dissolved oxygen (b) profiles at LO near-SP sampling site immediately outside of channel. Dashed profile lines represent post event sampling date; solid profiles are during event. Solid arrows indicate SP water flowing out of channel while patterned arrows represent upwelling LO water.


A. 2004 LO Near-SP Temperature
B. 2004 LO Near-SP Dissolved Oxygen
Depth (m)
0
0.5
1
1.5
2
2.5
3
11-Sep
12-Sep
14-Sep
21-Sep
8
10
12
14
16
18
Temperature (˚C)
6
7
8
9
10
Dissolved oxygen (mg/L)

oxygen content to that of the embayment (11 Sept. average SP Center site temp.:18.7˚C, DO: 7.1 mg/L) filled the upper half of the water column, and represented embayment water forced out into LO by storm runoff (Fig. 2.20 a-b).

Plankton, while spatially heterogeneous before the event, converged on a similar density value during this event at each of the SP sites. Both phytoplankton and zooplankton had statistically significantly different biovolume and biomass values at the different sites during pre-event sampling dates (Fig. 2.21a-b, one-way ANOVA comparing sites immediately pre-event on 8 Sept.: df = 3, phytoplankton $F = 652.968$, $p < 0.001$; zooplankton $F = 13.458$, $p = 0.015$). While already declining from mid-summer highs at the center site, both zooplankton and phytoplankton in SP continued to decline at all four sites during the combined precipitation and upwelling event to values that were not significantly different among sites during the event (one-way ANOVA comparing sites on 11 Sept.: phytoplankton df = 2 (missing Near-stream samples), $F = 1.666$, $p = 0.326$; zooplankton df = 3, $F = 1.231$, $p = 0.478$). While zooplankton populations had not recovered at any site post-event (one-way ANOVA comparing sites on 21 Sept.: df = 3, $F = 1.021$, $p = 0.472$; all post-hoc comparisons N.S.), or even a full month later (6 Oct., N.S. differences at any site), phytoplankton increased significantly at the center site within a week (Fig. 2.21a; one-way ANOVA comparing sites on 21 Sept.: df = 3, $F = 7.64$, $p = 0.039$; center site significantly higher than all three sites: post-hoc $p = 0.052$ compared to near-channel, $p = 0.055$ compared to near-stream, $p = 0.065$ compared to deep lobe; N.S. differences between other sites). This phytoplankton increase included diverse taxa including pennate and centric diatoms such as *Fragilaria* sp. and *Aulacoseira* sp., the chlorophyte *Chlamydomonas* sp., and the cyanobacteria *Anabaena* sp. and *Oscillatoria* sp.

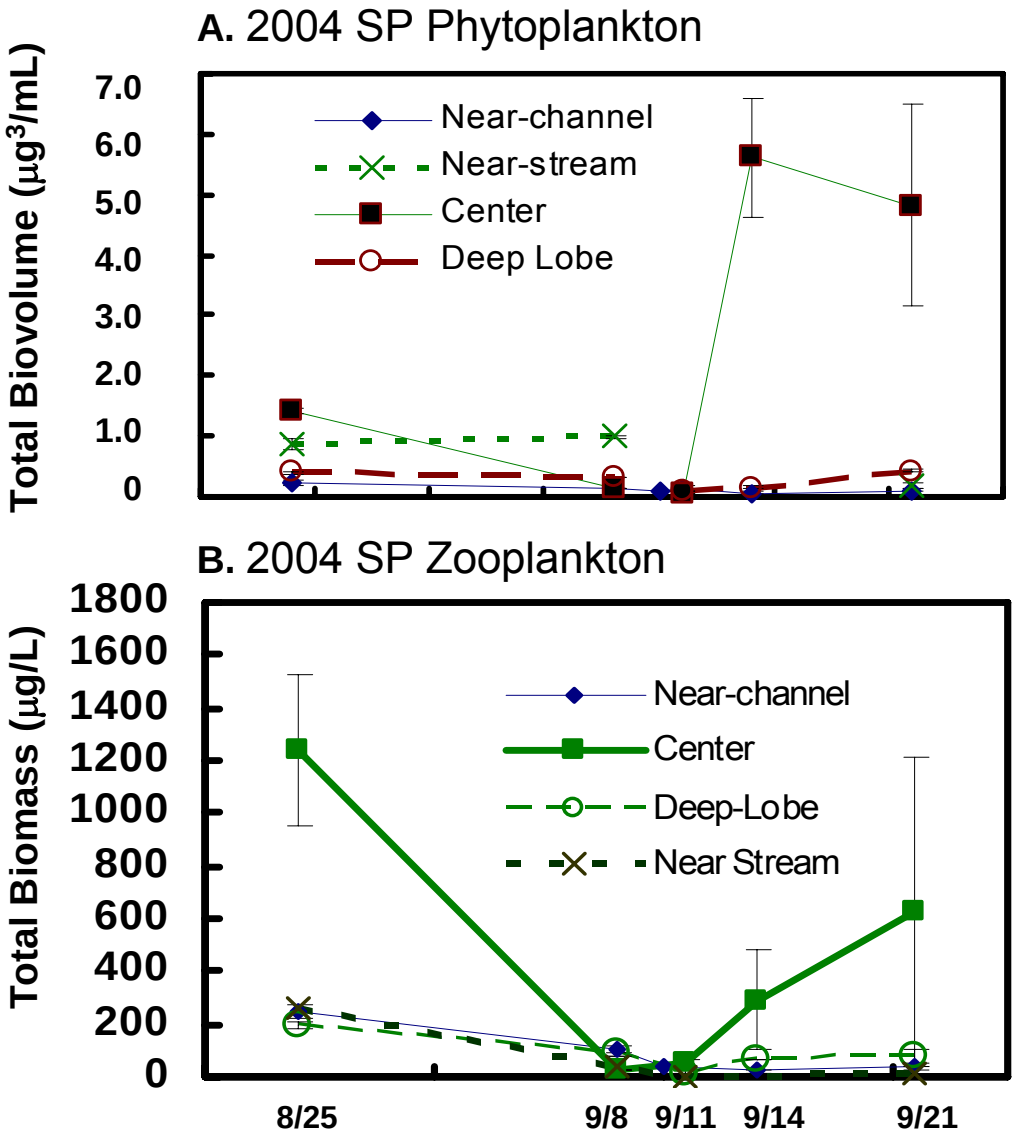


Figure 2.21 2004 phytoplankton biovolume (a) and zooplankton biomass (b) at four spatial sampling sites in SP. Sites sampled before (25 Aug., 8 Sept.), during (11 Sept.), and after (14 and 21 Sept.) upwelling and precipitation event. Error bars represent 1 s.e.

Discussion

Upwelling-driven exchange flow played an important role not only in initiating physical water exchange between Lake Ontario and its adjacent embayments, but also in mediating biological transport of organisms between these systems. The impact this external forcing had on the internal water-column dynamics of the embayment systems depended upon the duration of the upwelling event, the specific physical characteristics of the embayment, and the particular internal biological interactions that were already established within that embayment's plankton community. The final overall response of the embayments' plankton communities to each event was thus a result of the interaction between physical and biological forces—both those factors that serve to impact the system from outside, as well as internal processes that modify how the system responds to these outside influences.

Event duration

Our 25-year retrospective analysis of upwelling frequency in LO elucidates a pattern similar to that previously documented in the lake (Haffner 1984), which suggests that these events occur multiple times each year during the period of thermal stratification, sufficient to play an important role in the seasonal dynamics of adjacent embayments. We detected no noticeable temporal trend in the annual frequency of upwelling occurrences during the 25-year period we analyzed. Our data about the duration of these events documents the differential effects of sustained versus fleeting events. The potential impacts of two events per year lasting longer than four days (Fig. 4) on ecological dynamics has important implications for the LO near-shore and embayment habitats. Nevertheless, we did not observe any prolonged events during the two years of intensive sampling we conducted in 2003 and 2004. This could

indicate that our retrospective analysis did not account for all upwelling-inducing wind patterns, that these events are not as common as they appear in our dataset (or have become less common in the past decade due to meteorological shifts in characteristics like wind direction (Waples and Klump 2002)), or that the years of our intensive studies happened to be unusually free of prolonged upwelling events.

Little Sodus Bay: Buffered by volume, impacted by duration

The importance of event duration is illustrated by the differential effects we documented of shorter and longer-term upwellings on LSB and SP. Embayment volume played an important role in limiting the potential impact of upwellings in LSB, particularly those brief in nature. During the two short events in 2003 and 2004, LSB did not experience a measurable, system-wide response, nor did it show a distinct response to the precipitation that accompanied the second of the two events. Its large volume, coupled with its minimal connection to the terrestrial environment via its small watershed, essentially buffered this embayment from the effects of shorter-term upwelling events that did not last long enough to exchange large volumes of water. This is particularly true of impacts on the plankton community, because the nature of the density-driven flow from upwelling events typically occurs first along the sediment-water interface at the embayment bottom, which is many meters removed from the photosynthetically active surface waters of deeper water bodies like LSB.

The immediate impact of short-term events was not always restricted to the sediment-water interface in this larger-volume, stratified system, however. The 2002 event illustrates the potential that both short- and long-term events can have on systems like LSB. The minor upwelling that preceded the long-duration 2002 event (Fig. 2.3a) provides a clear example of how a very short event can drive exchange flow that can significantly impact the embayment photic zone. Because this upwelling

was not strong and did not result in the intrusion of a large amount of the cold deep LO water along the shoreline, the upwelling water was not cold enough to sink into the LSB hypolimnion, and instead it flowed along the thermocline, mixing in with the epilimnetic water (Fig. 2.7a-b). Estimates of displaced volume suggest that roughly 25% of the LSB epilimnion was replaced by LO water during this short event (Rueda and Cowen 2005).

The long-duration 2002 upwelling had a very different, and arguably stronger, effect on LSB than shorter events. Its increased duration and strength not only introduced a larger volume of LO water to the embayment, but also disrupted the late-summer thermal stratification of the system. While the shorter, epilimnion-restricted event preceding this one diluted the active photic zone with nutrient-poor water and hypolimnetic plankton from LO, the longer event had an effect more typical of in-lake upwelling dilution. In this case, the LSB epilimnetic water was forced out the channel into LO while the LSB hypolimnion was displaced upwards in the water column as colder LO water filled in along the bottom of the embayment (Fig. 2.5a, 2.7a-b). The effect of these large-volume exchanges would thus be to force nutrient-rich embayment hypolimnetic water (along with the associated plankton taxa) into the photic zone. The difference, however, is that the epilimnetic water that exited the embayment does not rock back following the event (as during a typical in-lake upwelling), and instead the newly introduced hypolimnetic embayment water is entrained in the photic zone. Depending on the extent of the event, the epilimnion may also not be completely displaced out of the embayment. The result is that photic zone plankton species may remain in the embayment, able to respond immediately to the nutrient influx from the hypolimnion. This characteristic distinguishes these events from typical in-lake upwellings by increasing the potential for longer-term impact. While the overall effect of in-lake upwelling on the plankton community has

been described in the literature with conflicting conclusions (Schelske et al. 1971, Gachter et al. 1974, Megard 1997), one reoccurring description of these physical forcing events is that they are transitory and isolated (e.g., Haffner et al. 1984). This is because thermal resistance can ensure these epi- and hypolimnetic water masses move past one another in the lake with little interaction, such that the original near-shore epilimnetic water mass eventually returns following the event, thus explaining the prevalence of reports discussing little net change between pre- and post-event plankton communities.

Sterling Pond: Buffered by macrophytes, impacted by precipitation

The potential impact of upwelling events is very different, however, for shallow, relatively small embayments where volume cannot buffer the impact of short-term events, nor entrain the intruding water. While event duration is not influential, embayment basin shape can still drive shallow embayment response to these upwelling events. Shallow bathymetry creates a different potential buffering factor: the dense macrophyte growth seen in SP. When an upwelling event was isolated, with low associated precipitation to drive tributary flow, exchange flow completely filled the water column of SP, replacing the resident biota. The net effect was more similar to the complete displacement of the near-shore epilimnion seen in nearshore LO (i.e., as seen in Figs. 2.11b, 2.15b) than the mixed water exchange in LSB. This was particularly true as post-upwelling rocking of water masses barotropically forced much of the near-channel water intrusion back out into LO. In SP we did not observe an upwelling-driven exchange flow event strong enough to penetrate the extensive macrophyte beds, and we saw no effect of upwelling intrusion in SP further into the embayment than the near-channel site. This was true both in 2003, as discussed above, but also in 2002, when we had similar retrospective data to that in LSB (at the

center sampling site only), yet saw no indication of upwelling impact at that site throughout the paired event. This suggests a spatially limited impact of these events, where the effect is constrained to a small portion of the system, especially because upwelling events can only occur in the late summer when LO is stratified, which is after dense macrophyte growth has filled much of the SP basin, isolating the center and near-stream sites from LO water entering through the channel.

The presence of a strong watershed connection via an extensive tributary also defined the relative importance of different forms of external forcing in highly connected SP, compared with LSB and its weak watershed connection. Whereas LO water and its associated biota were able to intrude into LSB to some extent during each of the events we studied, this was not the case for SP. Many of the late-summer winds that drive upwelling events in LO are accompanied by rain storms, as was the case for the 2004 hurricane-driven event. The strong tributary connection to the watershed made external forcing dynamics in SP more complex than for LSB. While the macrophyte buffer may provide a protective barrier for much of SP from the immediate impact of upwelling exchange flow from LO, this is not the case for tributary flow during high-precipitation events. In 2004, stream water from the tributary reached two-times the velocity of water entering the embayment from the 2003 upwelling exchange flow (Figs. 2.9, 2.5b). As seen in 2004, very cold upwelling LO water was located at the entrance of the SP channel, with a density capable of driving it into the channel and embayment as it did in 2003 (Fig. 2.20a), however, the force of the runoff coming from the tributary was so much stronger that it dominated the flow not only through the embayment but also throughout the water column of the channel. Unlike the upwelling flow of 2003, the physical forcing from the watershed was not noticeably constrained by the macrophytes, which were either flattened or pulled out of the sediment by high stream velocity. As a consequence, the tributary

flow was strong enough to flush all four of our SP sampling sites, resulting in a large-scale system-wide impact detectable throughout the plankton community with effects that lasted beyond the duration of the physical forcing (Fig. 2.21a-b).

Plankton community responses

Differential response: The impact of this macrophyte buffering is that many of the effects we observed at the Near-channel site in 2003 were fleeting, as was the accompanying upwelling event in LO. Again, it is likely that during this 2003 event much of the LO water intruding into SP encountered the macrophyte bed and then flowed back out of the embayment as the upwelling ceased in LO. Yet, this too was not an entirely transitory event. Rather, one major potential result of these events is the introduction of novel plankton to the embayment from LO (Fig. 15a-b), which though possibly small in number have the potential for strong lasting effects if these few introduced organisms were to establish successful populations. This is particularly true for the zooplankton, which can swim out of the intruding water and into the more protected parts of the embayment. While novel LO species were not detected in LSB during these events, phytoplankton and zooplankton were undoubtedly also introduced by upwelling exchange flow between LO and LSB. We did find the reverse: LSB phytoplankton species in LO near the channel immediately following the 2002 upwelling event, suggesting that near-shore LO may also be affected by organisms in the reverse exchange flow. However, the extent of impact on zooplankton dynamics of this exchange flow between LO and LSB, two predominantly limnetic systems, is likely small given that the two systems have most of their species in common. With the exception of the clear threat of newly introduced exotic species in the Great Lakes ecosystem being transported into the embayments, this exchange flow does not represent a significant pathway for the introduction of

species capable of dramatically shifting ecosystem dynamics in a relatively large pelagic embayment like LSB.

In contrast to LSB, SP, as a shallow, macrophyte-dominated ecosystem, has a distinctly different plankton community from LO. The 2003 upwelling event introduced at least 16 novel taxa into the embayment during the influx of upwelled water. Within the zooplankton, two new functional groups appeared – a large, efficient grazer, *D. retrocurva*, and a predatory cladoceran, *C. pengoi*, each capable of altering plankton dynamics through competition and predation respectively in a system dominated by rotifers and small cladocerans. *Cercopagis* additionally represents the spread of an exotic species. Although only *C. pengoi* was found in SP a few days after the initial introduction, both cladoceran species are capable of laying diapausing eggs that could lead to the future establishment of these species. .

Although we documented the short-term establishment of *C. pengoi* in SP, we did not find an established population of this species at any site in the succeeding three years that we sampled this embayment (Doyle-Morin, unpublished data). This result suggests that while the vector for invasion existed, something prevented it from successfully populating the embayment. *Cercopagis* is not typically found in shallow, littoral, fish-dominated systems (Rivier 1998) and so SP may not be ecologically suitable for it. However subsequent work has shown that another predatory cladoceran, *Polyphemus pediculus*, which has a large, late-summer populations in near-shore LO, and which is commonly found established in systems similar to SP (Wendel and Jüttner 1997, Halvorsen et al. 2004, Higgins et al. 2006, Sacherová et al. 2006, Ward and Whipple 1959, Lampert and Sommer 2007), also has not established in this embayment (Doyle-Morin, unpublished data). Macrophytes, which have been shown to affect survivorship and fecundity of other cladocerans negatively (Sutfeld et

al.1998, Burks et al. 2000, Cerbin et al. 2007) may play a role in the lack of success of *Polyphemus*, potentially serving as another biological buffer against the effect of upwelling events (Doyle-Morin, Chapter Three).

Common responses: While different upwelling events clearly varied in their effects on the LO and two embayments, we observed a number of commonalities, particularly in the overall plankton community response to physical forcing from exchange flow. In each event, in all three systems, both the phytoplankton and zooplankton communities were immediately diluted by the influx of hypolimnetic water into the photic zone. The extent of this dilution effect on the phytoplankton depended upon the species that were introduced into the photic zone with the hypolimnetic water, as large inedible taxa often increased at this time (countering the overall effect of dilution). Spring species, which often settle out of the system of stratified lakes during the warmer summer months (Reynolds 2006), commonly reappeared in these systems during exchange flow events, particularly large colonial diatoms like *Asterionella* sp. and *Fragilaria* sp. and mixotrophs like *Ceratium* sp. and *Dinobryon* sp. These species do not typically otherwise occur in the photic zone of these systems until fall overturn, when increased turbulence keeps them in contact with the photic zone and cooler temperatures reduce competition from faster growing summer species. The reemergence and growth of these cool-weather species during upwelling events has also been documented by others (Yaguchi 1977, Haffner et al. 1984).

Another general result of the exchange-flow events we documented was an increase in the availability of phytoplankton resources for grazers (with the minor exception of the short 2002 event, which was interrupted by the consecutive long upwelling). This result may explain why zooplankton populations exhibited more consistent patterns of abundance between events than phytoplankton. As seen in

previous research (Dunstall et al. 1990), copepods were the dominant component of the total zooplankton biomass during the majority of these events. However this pattern was not driven by an increase in the copepod populations, as discussed in Dunstall et al. (1990), but instead was the result of a consistent decrease in cladoceran populations during these events. The recovery of these grazing crustaceans, particularly *Daphnia* and *Bosmina*, also drove the post-event zooplankton biomass increases. This cladoceran response, particularly for the *Daphnia* species, may have resulted from the extent to which these grazers depend on abundant edible phytoplankton compared with copepods (Richman and Dodson 1983). It is noteworthy, however, that the population increase we documented occurred very quickly in some of these events (e.g., 2003 Lake Ontario (Fig. 2.11a) when a ten-fold biomass increase was found in less than three days), making it unclear if the population response that we saw was growth in response to environmental changes or simply the reintroduction of either offshore (LO) or undisturbed embayment water (LSB, SP). Given the significant increase compared with pre-event conditions, it seems likely that what occurred was a combination of both physical advection and biological dynamics.

Conclusion

We documented the short-term effects of upwelling exchange-flow events on two embayment ecosystems that differ in volume, depth, and watershed connectivity. Our findings show the potential impact of both physical and biological forcing from outside of the system, but also document the role that internal processes play in determining the extent of these external impacts on the overall response of resident plankton communities. This study also raises questions about the potential long-term impact of such exchange flows on these aquatic ecosystems, such as the role such late-

summer events play on biologically available nutrient (ie Si, SRP, NH_4) cycling in the photic zone both for the remainder of the current growing season as well as during the following spring overturn period, as well as the role of these events in the spread of exotic species. Water-level regulations, channel management decisions, and regional climate changes in the Great Lakes watershed will almost certainly affect the strength of future exchange events, altering the role these embayments play as intermediaries between the terrestrial watershed and the greater lake ecosystem.

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CHAPTER 3

THE BIOLOGICAL BARRIER: ASSESSING THE ROLE INTERSPECIFIC INTERACTIONS PLAY IN BUFFERING AGAINST INVADER ESTABLISHMENT IN A GREAT LAKES EMBAYMENT ECOSYSTEM

Introduction

Many systems retain distinct community identities despite strong connections and exchange with adjacent systems containing different assemblages of species. One such set of ecosystems are freshwater embayments located along the shorelines of larger water bodies, such as the Great Lakes. Embayments are often directly connected to these adjacent larger-bodied lakes via permanent water channels, and recent work has elucidated exchange flow processes that have driven the transport of native organisms through these channels (Doyle-Morin et al., Chapter 2). Unlike their marine counterparts, where strong salinity gradients can impose an osmotic barrier to successful biological transport between freshwater coastal embayments and the connected oceanic ecosystems, the exchange between two freshwater systems appears to offer less resistance to successful colonization. Yet, in many cases, transported organisms do not establish and the communities in these adjacent, connected systems remain distinct. The goal of our study is to explore what maintains community differences in the face of high levels of exchange. Specifically, we focused on the apparent exclusion of a potentially important predatory planktonic crustacean, *Polyphemus pediculus*, that is seasonally abundant in Lake Ontario but absent from a connected embayment, Sterling Pond, whose habitat appears to be quite suitable for its persistence.

As a part of a larger study of plankton dynamics in eight embayment ecosystems along the coast of Lake Ontario, we studied exchange flows between the lake and Sterling Pond, a small, shallow water body located in Fairhaven, NY. This embayment lies on the central southern coast and is connected to L. Ontario through a 30 m long, permanent man-made channel. We showed previously (Doyle-Morin et al., Chapter 2) that upwelling-driven exchange resulted in the inoculation into Sterling P. of 16 Lake Ontario zooplankton species not naturally present in the embayment. One of these novel species, the predatory cladoceran *Cercopagis pengoi*, remained in Sterling P. for as many as ten days after an exchange-flow event (Doyle-Morin et al., Chapter 2). The introduction of this species was particularly interesting because it represented the potential addition of a novel functional link (predatory cladoceran) to the food chain of this small embayment. At the same time, its transport represents both a pathway for the spread of an invasive species, but its ultimate failure to establish is an indication that the embayment plankton community is resistant to its invasion.

Much of the recent attention devoted to the role of predatory cladocerans in aquatic food webs has focused on species newly introduced to the North American Great Lakes and their watershed from their native habitats in the Baltic Sea region in the ballast water of ships (Mills et al. 1993, MacIsaac et al. 1999, Holeck et al. 2004, Duggan et al. 2005, Ricciardi 2006). The fact that these organisms can often represent an entirely novel link and functional role in pelagic food chains means that they have the potential to affect significantly resident populations not adapted to this type of predation pressure. Recent studies have documented the predatory impact moderately-sized taxa like *Cercopagis pengoi* have had on the small zooplankton of the lakes they have invaded (Benoît et al. 2002, Laxson et al. 2003, Gorokhova et al. 2005, Warner et al. 2006), while other studies have shown that larger taxa like *Bythotrephes*

longimanus may compete with zooplanktivorous fish for large prey, including other predatory zooplankton (Lehman 1991, Schulz and Yurista 1999). Other effects on the pelagic ecosystem have been documented for both species groups, including competition with native predatory invertebrates (Witt and Cáceres 2004, Põllumäe and Kotta 2007, Barbiero and Rockwell 2008, Foster and Sprules 2009), and cascading positive effects on phytoplankton through negative effects on grazers (Lehman 1991, Hovius et al. 2007).

The native Sterling P. pelagic zooplankton community, dominated by rotifers, small cladocerans, and copepod nauplii (Doyle-Morin et al., Chapter 1), appears to be well-suited for the diet of predatory cladocerans (Matveeva 1989, Packard 2001, Higgins et al. 2007, Põllumäe and Kotta 2007). A calculation of the likely frequency of upwelling events substantial enough to produce exchange flow carrying these predators into Sterling P. suggests on average 4.9 occurrences per year (Doyle-Morin et al., Chapter 2), yet extensive temporal and spatial sampling in this embayment during a recent six-year time period (2001-2006) did not reveal any successful establishment of a predatory cladoceran population (Doyle-Morin et al., Chapter 1, unpublished data). Whereas the absence of predatory invertebrates in the Sterling P. plankton may help to explain the high abundance of suitable prey, it also suggests that this zooplankton community could be especially vulnerable to successful introduction of a predatory invertebrate like *Cercopagis*.

The failure of *Cercopagis* to establish successfully in shallow, macrophyte-filled Sterling P. is perhaps not a surprise given that it naturally occurs exclusively in lakes large enough to have an extensive true pelagic zone (Rivier 1998). There is, however, a related predatory cladoceran, *Polyphemus pediculus* (like *Cercopagis,* a member of the Suborder Onychopoda) native to L. Ontario that frequently occurs as dense populations in the near-shore environment. Although it is difficult to determine

the average pelagic density of *Polyphemus* because of its characteristic swarming behavior (Young and Taylor 1990, Wendel and Juttner 1997) and seasonal migration between the limnetic and littoral zones in lakes (Haney 1980), we observed the greatest abundances along the near-shore (< 6 m of water) of L. Ontario in late summer (Doyle-Morin et al., unpublished data), at the time when the lake is strongly thermally stratified, summer storms are prevalent, and upwelling events are most likely (Doyle-Morin et al., Chapter 2). Thus, *Polyphemus* is abundant in near-shore L. Ontario in precisely the period that they are most likely to be carried into the embayment, and in fact, we have documented their presence in the near-shore zone during upwelling conditions in Lake Ontario (28 Aug 2002, 8.2 ˚C average water-column temperature, 0.02 *Polyphemus* L^{-1} density).

Prior research on *Polyphemus* suggests that it would be well-suited to living in Sterling P. as it is typically a littoral species, inhabiting shallow macrophyte-dominated habitats similar to that in this embayment (Wendel and Jüttner 1997, Halvorsen et al. 2004, Higgins et al. 2006, Sacherová et al. 2006, Ward and Whipple 1959, Lampert and Sommer 2007). Indeed, macrophytes undoubtedly provide a refuge for *Polyphemus* from predation by visually orienting zooplanktivorous fish that would cue in on their prey's large compound eye, as has been demonstrated for other cladocerans (c.f. Zaret 1972; Branstrator and Holl 2000). Rather than laying their diapausing eggs in the sediment or releasing them into the water column, *Polyphemus* have also been documented to lay their eggs preferentially on submersed aquatic vegetation, often on macrophyte stalks and the edges of leaves, suggesting another important role of the rooted plants in their natural habitat (Buttorina 2000).

Sterling Pond also contains the preferred prey of *Polyphemus*. As the smallest of the predatory cladocerans, *Polyphemus* is gape limited in the size of the prey that it can effectively manipulate with its feeding appendages, selectively consuming rotifers,

small cladocerans, and copepod nauplii (Matveeva 1989, Packard 2001, Higgins et al. 2007), all of which are abundant in the plankton of Sterling P. Nevertheless, despite "motive and opportunity", *Polyphemus* has not established a population in Sterling Pond.

The purpose of this study was to explore the factors that cause Sterling P. to remain resilient to the establishment of *Polyphemus*. The factor we considered to be most likely to limit *Polyphemus* establishment is fish predation, although the effect of macrophytes as a refuge might ameliorate this effect (Timms and Moss 1984, Schriver et al. 1995, Jeppesen et al. 1997, Burks 2002). The macrophyte-dominated Sterling P. habitat supports a large and diverse fish population dominated by planktivorous *Lepomis* spp. (e.g., *L. gibbosus*, *L. machrochirus*) and yellow perch (*Perca flavescens*), as well as piscivores (e.g., *Esox lucius*) and opportunistic bottom feeders such as the brown bullhead (*Ameiurus nebulosus*) (Arend 2008). It is unlikely for embayment water chemistry to have played a measurable role in keeping *Polyphemus* out, since this taxon has been shown to survive in a wide range of pH and nutrient conditions (Bērzinš and Bertilsson 1990). Similarly, the zooplankton community of Sterling P., as mentioned above, appears to be well suited for *Polyphemus*, as does the absence of many other planktonic predatory invertebrates that might otherwise be competitors. We tested each of these potential factors using mesocosm experiments: the suitability of embayment water for survival, resident embayment zooplankton both as potential prey and competitors, the effect of embayment zooplanktivorous fish, and the presence of macrophytes as a refuge from fish predation.

Methods

Study Site

Sterling Pond is a small (1.01 km^2 surface area), shallow (1.0 m median depth) embayment on the south shore of Lake Ontario near Fairhaven, New York. It is fed by Sterling Creek, which drains a large (203 km^2), agriculturally-dominated watershed providing a water retention time as short as five days during high rain events (Edwin T. Cowen, personal communication). The 140 m long channel that connects Sterling P. to L. Ontario is 2.5 m deep. The embayment's shallow depth and high nutrient and sediment loads from the watershed results in the growth of an extensive macrophyte bed that encompasses most of the basin except for a "deep lobe" area, 4 m deep, located to the east of the channel connection (see map in Doyle-Morin et al., Chapter 2).

Experimental Design

We ran two mesocosm experiments near the site of the deep lobe. The first, conducted from 2 to 10 August 2005, tested the effects of water source and the resident Sterling P. zooplankton community on *Polyphemus* survivorship and fecundity. The second, conducted from 1 to 8 August 2006, tested the effect of macrophytes and fish predation on *Polyphemus* survivorship and fecundity. August is the time of year when L. Ontario is stratified and introduction of *Polyphemus* by exchange flow to Sterling P. might be expected.

For the 2005 experiment, four combinations of L. Ontario and Sterling P. water and zooplankton were added to 12 mesocosms, with three replicates per treatment. The first treatment contained the natural assemblage of Sterling P. zooplankton in Sterling P. water. The second contained the natural assemblage of L. Ontario zooplankton in L. Ontario water. The third tested the effect of Sterling P. water (and

associated microbes and phytoplankton ≤ 75 μm) on *Polyphemus* survivorship, and contained 75 μm mesh filtered Sterling P. water with the natural L. Ontario zooplankton assemblage added (collected with a 75 μm mesh net) at natural density. The fourth tested the effect of the natural Sterling P. zooplankton assemblage on *Polyphemus* as both potential prey and competitors. This treatment contained 75 μm filtered Sterling P. water, and half-ambient densities each of L. Ontario and Sterling P. zooplankton assemblages.

Mesocosms were constructed out of plastic cylinders open at the top and closed at the bottom, each 2 m tall, 1 m in diameter. They were deployed in two sets of six, and connected to floating wooden braces anchored in place at a depth where the cylinders were suspended at least 1/3 m above the sediment. The 12 mesocosms were assigned in triplicate to the four different treatments, with replicates blocked according to location, assigned to each side of the two floating beams, ensuring that no two were directly across from each other. Each mesocosm was first filled with 150 L of 75 □m filtered lake water from either the center of Sterling P. or nearshore L. Ontario, depending on treatment. Zooplankton were collected throughout the water column (0 – 6 m in near-shore L. Ontario, 0 – 3 m in Sterling P.) using a Clarke-Bumpus quantitative sampler fitted with a 75 μm mesh net, and gently mixed into mesocosms at ambient density. The L. Ontario zooplankton assemblage was examined to confirm the presence of *Polyphemus*. Three replicates of an equal volume of the dense zooplankton water added to each treatment were filtered through a 75 μm mesh cup and preserved in 70% ethanol. These samples were used to estimate initial zooplankton densities added to each mesocosm. Samples for initial phytoplankton density (100 mL) were taken from each mesocosm and preserved in a 1% Lugols solution. Netting (1 mm mesh) was secured over the mesocosms to exclude birds, large insects and litter fall (though the nearest trees were at least 150 m away).

Mesocosms were thoroughly but gently mixed twice daily using a small paddle. Throughout the course of the experiment temperature and dissolved oxygen were measured (Yellow Springs Instruments, Model 54) at the surface and bottom of each mesocosm each morning prior to mixing.

The 2006 experiment was also comprised of four treatments, (four replicates per treatment) in a 2 × 2 design with macrophyte presence or absence (hereafter +Macrophytes or -Macrophytes) crossed with fish presence or absence (hereafter +Fish or -Fish). All mesocosms were filled with 180 L of ambient Sterling P. water (unfiltered) to which L. Ontario zooplankton at natural density (collected as in the 2005 experiment) was added. Macrophytes from the center of Sterling P. were added to eight of the mesocosms. *Ceratophyllum demersum, Nitellopsis obtusa, Elodea canadensis*, and *Myriophyllum spicatum*, the naturally abundant species in Sterling P., were added at a mean of 14.5 stems (range 13-19) per mesocosm. Before being introduced, the macrophytes were rinsed in filtered lake water, and the base of each stem was weighed down with a small bag filled with clean lake rocks. Immature sunfish (*Lepomis* sp.) were collected using baited minnow traps in Sterling P. and added to the mesocosms on the second day of the experiment. Two sunfish, 3.5 - 4 cm SL, were added to each of four mesocosms without macrophytes and four with macrophytes. Three samples of 180 L of Sterling P. water, filtered through a 75 μm mesh, were preserved for initial zooplankton densities. Three samples of the L. Ontario zooplankton water were also preserved for initial densities.

Prior to adding the fish on 3 Aug., dissolved oxygen and temperature measurements were taken from each mesocosm. Ten liters of water collected from the middle of each well-mixed mesocosm were filtered through a 75 □m mesh for initial zooplankton determination (preserved in 70% ethanol), and the filtered water was returned to each mesocosm. A phytoplankton sample (100 mL, 1% Lugols

preservation) was also collected from each mesocosm. The fish were added after sampling was completed. Temperature and dissolved oxygen were measured daily, after which each mesocosm was mixed gently with a paddle and checked twice daily throughout the experiment for live, active fish. Zooplankton and phytoplankton samples (as at the start) were collected and preserved 24 h following the addition of the fish to assess the immediate impact of the fish predation, for a total of four plankton sampling dates (experiment start, before and after fish addition, experiment end).

The 2005 experiment ran for seven days, and the 2006 experiment for five days after the addition of the fish. At the conclusion of each experiment, mesocosms were mixed and a 100 mL sample was collected from each for phytoplankton identification and enumeration. Most taxa were identified to species when possible, and at least to genus, except for small flagellates. The remaining water from each mesocosm was then filtered through a 75 μm mesh for final zooplankton enumeration. At the end of the 2006 experiment, fish length was measured and recorded, and macrophytes (which were floating and intact) were indentified to species, rinsed with 75 μm filtered lake water, inspected for the presence of littoral invertebrates, and dried (60 °C for two days) for determination of dry weights.

Zooplankton samples were processed in the laboratory, using an Olympus SZH10 stereo-dissecting scope and an Olympus BH-2 compound scope to identify organisms to species (genus for some rotifers). All samples were subsampled, and at least 100 total organisms were identified and counted. Entire samples were then analyzed for abundance of predatory invertebrates and any rare species not found in the subsamples. *Polyphemus* individuals were measured to the nearest 0.10 μm using an eyepiece micrometer.

Statistical analyses

Normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test) of each data set was assessed. Temperature and dissolved oxygen measurements (except 10 August 2006 when no dissolved oxygen data were collected) were compared among replicates and with the Sterling P. water column to determine the extent to which environmental conditions in the mesocosms deviated from the natural environment. Because dissolved oxygen data were not Normal and transformation did not improve Normality, Kruskal-Wallis tests were used for temperature and dissolved oxygen measurements. A nonparametric Mann-Whitney test was used for all two-sample temperature and dissolved oxygen comparisons, including post-hoc Kruskal-Wallis comparisons.

Zooplankton treatment responses were assessed using either one- or two-way ANOVA, with Bonferroni-adjusted α-values for individual comparisons. The *Polyphemus* data from 2006 were square-root transformed to adjust for a large number of zero values. All error estimates reported are ± 1 standard error. *Bythotrephes* from L. Ontario, a potential predator of *Polyphemus*, was found alive in two of the 2006 mesocosms (one +Macrophyte/-Fish treatment and one -Macrophyte/-Fish treatment). Because the presence of this additional potential predatory pressure is a confounding variable, data from those two mesocosms were not used and statistical analyses employed an unbalanced design. Statistical analyses were carried out using Minitab, version 15.1 (2007) and SPSS, version 16.0 (2007).

Results

Experimental conditions

Temperature and dissolved oxygen in the mesocosms were not vertically stratified in the 2005 experiment, while in the 2006 experiment surface values were slightly warmer and less oxygen-rich than bottom values in 2006 (Table 3.1, Mann-Whitney U test, $Z = -2.173$, $p = 0.030$ for temperature, $Z = -2.496$, $p = 0.013$ for dissolved oxygen). For both years, temperature ranged between 23.7 and 29.6 °C throughout the water column, and dissolved oxygen ranged from 5.4 to 12.6 mg L^{-1} in the surface waters and from 6.1 to 14.9 mg L^{-1} in the bottom water of the mesocosms, depending upon the time of day the measurement was taken (low values occurred during morning sampling and high values in the afternoon, thus driven by photosynthesis).

There were significant differences in dissolved oxygen concentration among treatments in both the 2005 and 2006 experiments (Table 3.2, Kruskal-Wallis Test $\chi^2 = 15.85$, $p = 0.001$ for 2005; $\chi^2 = 136.0$, $p < 0.001$ for 2006), and for temperature in 2005 (Kruskal-Wallis test $\chi^2 = 8.85$, $p = 0.031$). Temperature in 2006 did not vary significantly among treatments (Kruskal-Wallis test $\chi^2 = 0.220$, $p = 0.947$). Post-hoc tests for 2005 showed that temperatures in the treatments containing L. Ontario water were significantly higher than in other treatments, and that the Sterling P. zooplankton treatment was significantly higher in dissolved oxygen than the other treatments. Although they are statistically significant, the differences were only 0.6 °C and 0.5 mg L^{-1} respectively, and so likely not ecologically important. In 2006, mesocosms containing macrophyte treatments were significantly higher in dissolved oxygen concentration, by 2.5 mg DO L^{-1}, than those containing treatments without macrophytes (Table 3.2, Mann-Whitney U test $Z = -9.97$, $p < 0.001$). Water

Table 3.1 Mean 2005 and 2006 temperature and dissolved oxygen at the surface and bottom of the experimental mesocosms (± 1 SE). Asterisks indicate significant differences between depths ($p < 0.05$).

	2005 Temp. °C	2006 Temp. °C	2005 D.O. mg/L	2006 D.O. mg/L
Surface	**26.5 ± 0.2**	**27.0 ± 0.1***	**8.0 ± 0.2**	**9.9 ± 0.2***
Bottom	**26.3 ± 0.2**	**26.6 ± 0.2***	**9.7 ± 0.2**	**9.1 ± 0.2***

Table 3.2 2005 (a) and 2006 (b) temperature and dissolved oxygen for each treatment, averaged among the experimental replicates (± 1 SE). Asterisks indicate significant differences among treatments ($p < 0.05$).

a	2005 Temp. °C	2005 D.O. mg/L
SP water & SP zoop.	26.4 ± 0.2*	7.2 ± 0.3*
LO water & LO zoop.	27.0 ± 0.3*	7.5 ± 0.1*
SP water & LO zoop.	26.2 ± 0.3*	7.2 ± 0.2*
SP water & LO/SP zoop.	26.1 ± 0.3*	8.0 ± 0.1*

b	2006 Temp. °C	2006 D.O. mg/L
- Fish - Macrophytes	26.7 ± 0.2*	8.5 ± 0.1*
-Fish + Macrophytes	26.7 ± 0.2*	10.9 ± 0.2*
+ Fish - Macrophytes	26.7 ± 0.2*	8.6 ± 0.1*
+ Fish + Macrophytes	26.8 ± 0.2*	11.2 ± 0.2*

temperature did not differ significantly between the inside and outside of the mesocosms in either experiment, but dissolved oxygen was significantly lower in the mesocosms than in the surrounding water column in 2005, while it was slightly higher inside of the mesocosms than in the surrounding lake water in 2006 (Table 3.3, t-test, $t = 5.782$, $p < 0.001$ in 2005; $t = -6.100$, $p < 0.001$ in 2006).

Treatment effects

Polyphemus survivorship

Polyphemus survived and reproduced in both experiments. In 2005, *Polyphemus* densities in the water inoculated from L. Ontario were low (mean = 0.017 *Polyphemus* L^{-1} across replicates containing L. Ontario water) and patchily distributed with only one-third of both initial and final experimental replicates containing *Polyphemus*. Final densities in those Sterling P. mesocosms that initially contained *Polyphemus* (both Sterling P. water and Sterling P. zooplankton treatments) averaged 0.057 individuals L^{-1} resulting in a mean rate of increase of 0.17 day^{-1}. In the single mesocosm of L. Ontario water with L. Ontario zooplankton that contained *Polyphemus,* the *Polyphemus* density also increased slightly over the course of the experiment to 0.133 individuals L^{-1} at a rate of 0.27 day^{-1}.

Inoculated *Polyphemus* densities were substantially higher in the 2006 experiment than in 2005, averaging 0.52 (± 0.1 SE) individuals L^{-1} in the three initial L. Ontario addition replicates. On the day following the fish addition, there was significant variation in *Polyphemus* density among treatments (One-way ANOVA, $F = 4.060$, $df = 3$, $p = 0.040$). This result was driven by the -Macrophyte/-Fish treatment, which had a significantly higher average density (0.57 ± 0.2 *Polyphemus* L^{-1}) than the

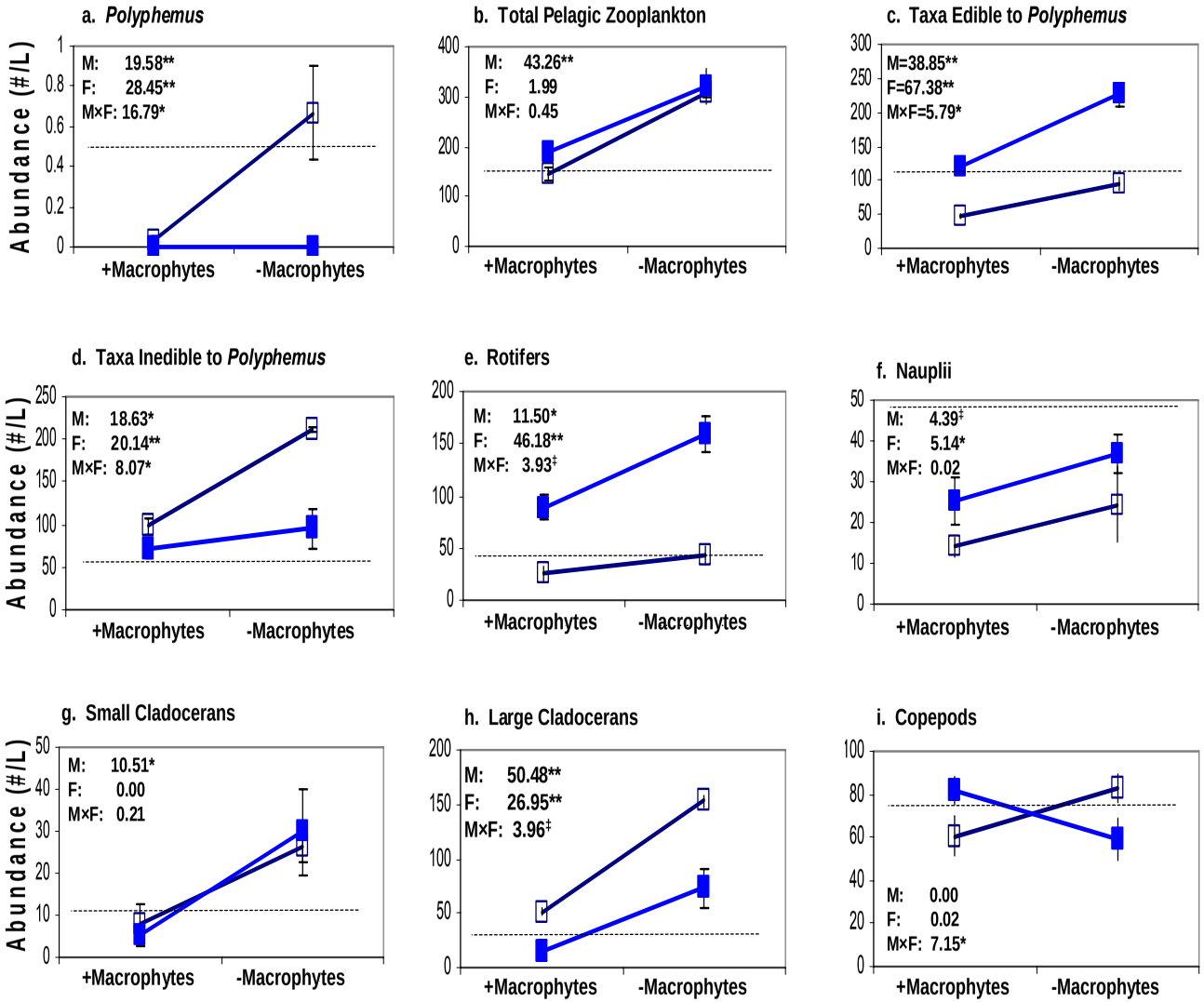
Table 3.3 Mean 2005 and 2006 temperature and dissolved oxygen outside (in Sterling P.) and inside of the experimental mesocosms (± 1 SE). Asterisks indicate significant differences between outside and inside of mesocosms ($p < 0.05$).

	2005 Temp. °C	2006 Temp. °C	2005 D.O. mg/L	2006 D.O. mg/L
Outside	**26.4 ± 0.3**	**27.2 ± 0.2**	**10.4 ± 0.5***	**7.9 ± 0.3***
Inside	**26.4 ± 0.1**	**26.7 ± 0.1**	**7.5 ± 0.1***	**9.7 ± 0.1***

+Macrophyte/ +Fish treatment (Bonferroni-adjusted t-test, p = 0.045). The +Macrophytes/-Fish and -Macrophytes/+Fish treatments did not differ in *Polyphemus* densities from the -Macrophyte/-Fish treatment at this point (Bonferroni-adjusted t-test, p = 0.189, p = 0.168 respectively), and no other comparisons were significant. The +Macrophyte/+Fish treatment was the only one to show any evidence of a decline in overall *Polyphemus* density (final mean = 0.25 ± 0.25 *Polyphemus* L^{-1} from the initial inoculation densities, though the change was not significant (Bonferroni-adjusted t-test, p = 0.182; all other comparisons, p > 0.50).

At the end of the experiment, five days after fish addition, *Polyphemus* densities showed significant treatment and interaction effects (Fig. 3.1a). Densities in the -Macrophyte/-Fish treatment (0.67 ± 0.23 individuals L^{-1}) were significantly greater than in any of the other three treatments (Bonferroni adjusted t-test, p = 0.004 vs. -Macrophyte/+Fish, p = 0.009 vs. +Macrophyte/-Fish, p = 0.004 vs. +Macrophyte/+Fish). There are no statistical differences between any of the other treatments: with macrophytes, with fish or with both (Bonferroni-adjusted t-test, p = 1.000 for all comparisons). While *Polyphemus* density had not significantly changed from initial densities (dashed line in Fig. 3.1) in the -Macrophyte/-Fish treatment (Bonferroni-adjusted t-test, p = 1.000), densities were either marginally significantly lower than initial densities in all other treatments (Bonferroni-adjusted t-test, p = 0.062 for -Macrophyte/+Fish; p = 0.060 vs. +Macrophyte/+Fish), or not significant (p = 0.113 for +Macrophyte/-Fish). The -Macrophyte/-Fish treatments were the only mesocosms not to show a negative *Polyphemus* population growth rate over the course of the experiment (Fig. 3.2).

Figure 3.1 Final abundance of various zooplankton groups in 2006 as a function of treatment. Closed symbols: +Fish; open symbols: -Fish (± 1 SE). Results of 2-way ANOVAs are listed as F-values for both treatments and interaction effects; df = 1 for all tests. Asterisks indicate significant effects; * = $p \leq 0.05$, ** = $p \leq 0.001$, ‡ = $p \leqq 0.10$. Starting densities are shown with dashed line on each graph.


a. Polyphemus
Abundance (#/L)
M: 19.58**
F: 28.45**
M×F: 16.79*
+Macrophytes
-Macrophytes
b. Total Pelagic Zooplankton
M: 43.26**
F: 1.99
M×F: 0.45
+Macrophytes
-Macrophytes
c. Taxa Edible to Polyphemus
M=38.85**
F=67.38**
M×F=5.79*
+Macrophytes
-Macrophytes
d. Taxa Inedible to Polyphemus
Abundance (#/L)
M: 18.63*
F: 20.14**
M×F: 8.07*
+Macrophytes
-Macrophytes
e. Rotifers
M: 11.50*
F: 46.18**
M×F: 3.93‡
+Macrophytes
-Macrophytes
f. Nauplii
M: 4.39‡
F: 5.14*
M×F: 0.02
+Macrophytes
-Macrophytes
g. Small Cladocerans
Abundance (#/L)
M: 10.51*
F: 0.00
M×F: 0.21
+Macrophytes
-Macrophytes
h. Large Cladocerans
M: 50.48**
F: 26.95**
M×F: 3.96‡
+Macrophytes
-Macrophytes
i. Copepods
M: 0.00
F: 0.02
M×F: 7.15*
+Macrophytes
-Macrophytes

Impact on zooplankton prey community

There was a significant increase in overall zooplankton density in treatments containing macrophytes versus those without macrophytes, but no difference between treatments with and without fish, and no interaction effect (Fig. 3.1b). When the zooplankton community is broken down into functional groups, copepodids were the only group not to exhibit a significant effect of either the fish or the macrophyte treatments, however they did show a significant interaction effect (Fig. 3.1i), though the reason for this is obscure.

For zooplankton within the size range edible to *Polyphemus*, including rotifers, small cladocerans, and copepod nauplii, there were highly significant effects of the macrophyte and fish treatments with densities greater in the absence of macrophytes and the absence of fish. The interaction effect was also significant, with density differences between the +Fish and –Fish treatments greater in the absence of macrophytes (Fig. 3.1c). When broken down into the three taxonomic groups edible to *Polyphemus*, only rotifer density had significant effects that mirrored the "total edible zooplankton" group as a whole, although the interaction effect was only marginally significant (Fig. 3.1e). This is unsurprising given that rotifers were an order of magnitude greater in density than small cladocerans or nauplii. All three of these taxonomic groups were significantly more dense in the -Macrophyte treatments (nauplii only marginally significant), while rotifers and nauplii were also more dense in the +Fish treatments (Fig. 3.1e-g).

Taxa that are presumably too large to be vulnerable to *Polyphemus* predation (i.e., large cladocerans, copepodids) also showed significant treatment effects when pooled as a group, with densities greater in the -Macrophyte and -Fish treatments, and a significant interaction effect such that densities were greatest in the absence of both

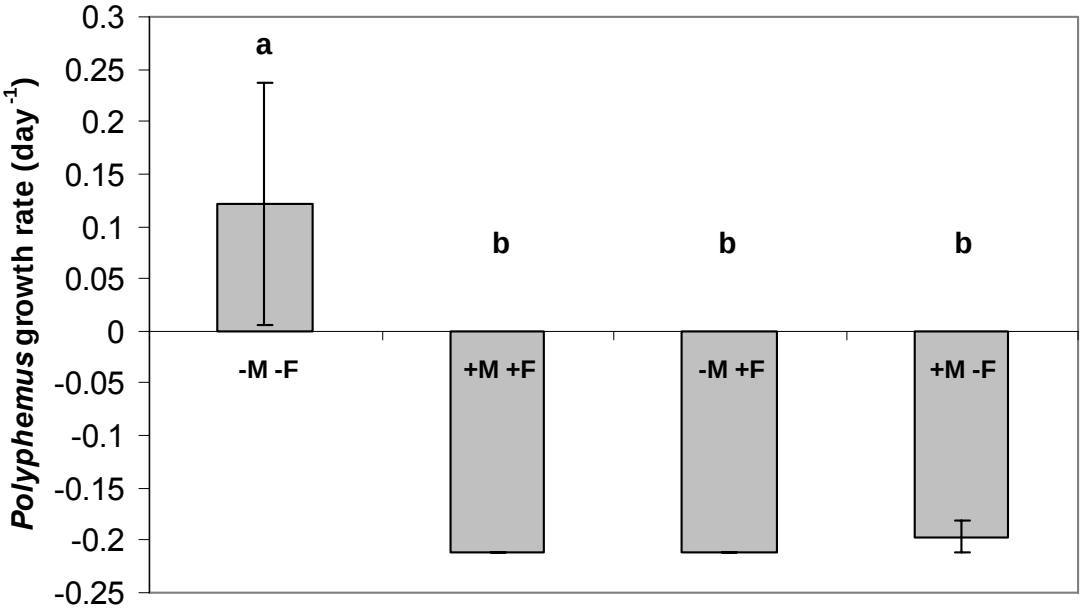


Figure 3.2 *Polyphemus* growth rate during the 2006 feeding experiment. Rates differ among treatments, with "a" and "b" representing significantly different treatments *(ANOVA*: df = 3, F = 10.35, p = 0.002). Error bars: ± 1 SE. Low variance in +M+F and –M+F treatments due to almost complete mortality (-M+F: one replicate with two surviving individuals).

macrophytes and fish (Fig. 3.1d). This pattern is driven predominantly by the large cladocerans which mirror the "inedible" group as a whole, but with only a marginally significant interaction; copepodids showed no significant response to either treatment, but did contribute to the interaction effect (Fig. 3.1h,i).

Polyphemus predators

Although not a part of the experimental design, potential planktonic predators of *Polyphemus* were present in L. Ontario during both experimental time periods, and thus were added to the mesocosms as part of the ambient L. Ontario zooplankton in both experiments. *Cercopagis pengoi* and *Leptodora kindti* were found in over half of the initial samples in 2005 at a mean total density of 0.012 (± 0.006) predatory invertebrates L^{-1}. None of these additional inoculated predatory invertebrates were found in the final mesocosm samples in 2005. *Cercopagis* and *Leptodora* were also found in initial samples in 2006, along with *Bythotrephes longimanus.* Unlike 2005, some of these predatory invertebrates were also found in the final mesocosm samples. *Leptodora* and *Bythotrephes* were found in several mesocosms both during and at the end of the experiment. *Chaoborus punctipennis* was also found in two final mesocosm samples. With the exception of a single *Bythotrephes* found in a +Macrophyte mesocosm, all additional predatory invertebrates found at the conclusion of the experiment were in the -Macrophyte/-Fish mesocosms. The mean length of the fish added to the +Fish mesocosms was 3.79 cm (± 0.09 SE), and did not vary significantly among treatments.

Discussion

Increases in *Polyphemus* densities in water from Sterling P. both in 2005 and 2006 showed that *Polyphemus* survival and reproduction is not negatively affected by the quality of the embayment water itself and so is not excluded from establishing in the embayment by features of the water distinct from those of Lake Ontario. However, low ambient *Polyphemus* densities in L. Ontario during the 2005 study limited our ability to draw conclusions from that experiment. The results of the 2006 experiment show that, as hypothesized, fish predation had a strong negative effect on *Polyphemus* persistence in Sterling P. In addition, however, we obtained the unexpected result that the presence of macrophytes not only did not provide a refuge from fish predation, but in fact had a negative effect on *Polyphemus* in both the presence and absence of the fish predation.

Zooplankton samples collected 24 hours after the fish were introduced did not reveal any predation effect, presumably because insufficient time had elapsed, however the *Polyphemus* population was significantly reduced by the end of the experiment, four days later. Macrophytes also did not serve as an effective refuge against predation for any of the other zooplankton taxa present in the mesocosms. Rather, plankton densities were uniformly either reduced in the presence of macrophytes, or in the case of copepodids, not affected. Where there were significant interaction effects between the fish and macrophyte treatments for taxa vulnerable to fish predation (i.e., *Polyphemus* and large cladocerans), densities and density differences between -Fish and +Fish treatments were greatest in the absence of macrophytes. Even in the absence of fish, the presence of macrophytes led to substantial decline in the *Polyphemus* population. This negative macrophyte effect was not immediate, exhibiting a slight but not statistically significant reduction in

Polyphemus after three days (24 hours following fish introduction), but a completely decimated population by the end of the experiment.

There are a number of possible explanations for this negative effect of the macrophytes. Macrophytes may have produced an allelopathic chemical that negatively affected the *Polyphemus*. In one extreme case, Sutfeld et al. (1996) found complete mortality of *Daphnia magna* after five days of exposure to exudates from the macrophyte *Nuphar lutea*, though these are taxa not present in our study. Several studies have, however, shown that two of the macrophyte taxa used in our study, *Elodea* and *Myriophyllum*, release chemicals that induce *Daphnia* species to avoid dense macrophyte beds (Pennak 1973, Dorgelo and Heykoop 1985). Although subsequent studies showed that this negative behavioral response is suppressed in the presence of fish kairomones, suggesting that fish predation is a stronger pressure on the cladocerans (Lauridsen and Lodge 1996, Jepperson et al. 1997), authors of some recent studies have found that the presence of macrophytes leads to earlier maturation times and, as a result, smaller body and clutch sizes of cladocerans (Burks et al. 2000, Cerbin et al. 2007). If this were the case in our system, it would explain the lower abundance of *Polyphemus* and large cladocerans in the macrophyte treatments at the end of the experiment.

The reduced abundance of total zooplankton in the macrophyte treatments in 2006 suggests that the *Polyphemus* population may have been indirectly negatively affected by the negative effects of macrophytes on phytoplankton (van Donk and van de Bund 2002, Bauer et al. 2009) which would ultimately reduce the density of the *Polyphemus* prey population. This would explain the lower densities of small zooplankton edible to *Polyphemus* in the +Macrophyte treatments (Fig. 3.1c). In addition, there may have been competition between the pelagic zooplankton enumerated in our study and macrophyte-associated benthic cladocerans that we found

associated with macrophytes in our mesocosms (i.e., *Sida crystallina* and *Simocephalus* sp.) which can exert extensive grazing pressure on phytoplankton (Stansfield et al. 1997).

Finally, although we mixed the mesocosms twice daily, an artificial constraint of this environment may be a relative lack of physical mixing compared with the embayment itself. Stagnation would reduce the suspension of phytoplankton and as a result, cells may have settled to the bottom where they would be unavailable for consumption by zooplankton. For example, a phytoplankton cell sinking at a rate of 25 $\mu m\ sec^{-1}$ (smaller cell from Table 2.5 in Reynolds 2006) would sink 1.08 m in the course of the 12-hour period between our mixing efforts, settling near the bottom even if it started at the top of the water column. This effect would presumably be magnified by the presence of macrophytes, which provide physical surfaces throughout the water column on which the phytoplankton can settle. Together, these indirect effects of macrophytes on the availability of prey for *Polyphemus* could explain their gradual decrease in the +Macrophyte treatments, as well as the low density of *Polyphemus* at the end of the experiment.

While not directly assessed by the design of this experiment, cladoceran predation may have had a negative effect on *Polyphemus*. No *Polyphemus* was found alive in the mesocom that contained five *Bythotrephes* at the end of the experiment, suggesting that *Polyphemus* is susceptible to predation by this voracious cladoceran (Schulz and Yurista 1999). No such pattern was seen in mesocosms containing either *Leptodora* or *Chaoborus*, presumably because *Polyphemus* is too large to be effectively preyed upon by them. While these two predators are strongly size-limited by the morphology of their feeding baskets and antennal gapes respectively, *Bythotrephes* has been shown to grasp and shred its prey (Schulz and Yurista 1999), and so could consume even larger *Polyphemus* individuals. Interestingly, these other

predatory cladocerans (*Leptodora* and *Bythotrephes*) were only found in the -Macrophyte/-Fish mesocosms, suggesting that the same factors causing poor *Polyphemus* survivorship in Sterling P. may also have a negative effect on other predatory cladocerans introduced from L. Ontario.

Finally, this study provided us with data on the potential impact of *Polyphemus* on the Sterling P. plankton community, were this species able to establish successfully. Zooplankton categorized as too large to be susceptible to *Polyphemus* predation showed treatment effects similar to those of *Polyphemus*. The large cladocerans that dominate this grouping, *Diaphanasoma* sp. and *Ceriodaphnia* sp., are large enough to be easily seen by the small planktivorous fish dominant in this system. Like *Polyphemus,* while their particular sensitivity to macrophyte allelochemicals has not been studied, these cladocerans are also taxonomically related to the daphniids typically used in such studies (eg. Burks et al. 2000, Cerbin et al. 2007), and could be expected to respond similarly.

The fact that the taxa susceptible to *Polyphemus* predation (nauplii, rotifers, and small cladocerans) were most abundant in the -Macrophyte/+Fish treatment may have been the result of two factors acting in concert. These smaller animals (in particular, the rotifers and nauplii) are not large enough to be vulnerable to predation by fish, and as a result, they are released from both (1) competition with large cladocerans and from (2) predation by *Polyphemus* relative to the –Fish treatments where their competitors and predators were abundant.

With the additional physical connection they have to their adjacent large lakes, freshwater embayment ecosystems appear to be more vulnerable to outside influences than fully-enclosed lake and pond ecosystems. This may be particularly true of influences in the form of biological invasions for embayments located along the shoreline of the North American Great Lakes, which have been inundated in recent

years by a wealth of exotic and invasive species (Mills et al. 1993, MacIsaac et al. 1999, Holeck et al. 2004, Duggan et al. 2005, Ricciardi 2006). Our study suggests, however, that these embayment systems contain biological vectors that prevent establishment of some invaders, and ameliorate the potentially strong detrimental role that newly introduced species like *Polyphemus* could have on the native flora and fauna of such systems.

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